

BIONOMICS AND ECOLOGY OF Ornithodoros (P.) turicata
americanus (MARX) (IXODOIDEA: ARGASIDAE)
AND OTHER COMMENSAL INVERTEBRATES PRESENT IN THE
BURROWS OF THE GOPHER TORTOISE, Gopherus polyphemus DAUDIN

BY

ERIC GORDON MILSTREY

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL OF THE
UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1987

To Susan, my wife,
and my son, Tristan.

ACKNOWLEDGEMENTS

I want to express my sincerest thanks to Dr. J.F. Butler for his help, guidance and thoughtful discussion on my work. I thank him and the USDA for the grant that funded this research.

Thanks go to Diana Simon, Debbie Boyd, Rick Wilkerson, Sam Telford, Andy Beck, Ben Beard and the rest of the wonderful people with whom I have worked with for the past six years. You have made my stay enjoyable and professionally profitable.

I am grateful to Mr. Irving Roberts and Mr. G.W. Schlitzkus of Owens-Illinois for allowing this research to be done on their lands.

Special thanks go to Ms. Joan Diemer of the Florida Game and Freshwater Fish Commission, Wildlife Research Unit in Gainesville. Her insight, good humor and instruction on the gopher tortoise and its habits proved to be invaluable. There are very few researchers who are as cooperative.

There were a large number of individual experts that were consulted during the course of this study, too many to mention here, and all should be individually acknowledged but four stand out as being most helpful: Dr. Dale Habeck for his interest and expertise with rearing immature insects, Dr. R. Woodruff for his discussions on beetles,

and their interactions and for his paper on the invertebrates of the gopher burrow, Mr. D. Franz who served as my major consultant on the vertebrates present in gopher tortoise burrows and Dr. S.C. Zam for his assistance on the immunological aspects of this work.

My most profound and deepest thanks go to my wife Susan for her support through this endeavor. She kept my morale high and was my primary motivator. I acknowledge her commitment to my degree as was demonstrated, by her raising our son, helping me and working full-time so that we were financially secure. Her typing and editorial skills were greatly appreciated during manuscript preparations.

TABLE OF CONTENTS

	<u>Page</u>
ACKNOWLEDGEMENTS	iii
LIST OF TABLES	vii
LIST OF FIGURES	xi
ABSTRACT	xii
CHAPTERS	
I INTRODUCTION	1
II ARGASID NICHE SPECIALIZATION IN RELATION TO SYSTEMATICS AND PATHOGEN TRANSMISSION . . .	11
Historical Perspective: Ticks as Disease Agents	11
Classification of the Ixodoidea	13
Morphology	13
Developmental and Behavioral Characteristics	14
Systematics of Argasidae	16
Genus: <u>Argas</u>	26
Genus: <u>Ornithodoros</u>	29
Small Genera: <u>Otobius</u> , <u>Antricola</u> , and <u>Nothaspis</u>	34
Life Cycles: Laboratory and Field	35
<u>Argas</u>	35
<u>Ornithodoros</u>	37
<u>Antricola</u> and <u>Nothaspis</u>	42
Ecological Niches Utilized by the Argasidae . .	42
Troglodytic Niches	42
Niticolous Habitats	43
Free Living Hosts	44
Pathogens Associated with Argasid Ticks . . .	44
Burrow Habitats	46
Caves and Shelters	57
Sheds and Houses	58
Shallow Caves and Overhangs	63
Deep Caves	64
Nests	67
Marine nests	67
Ground or cliff nests	71
Arboreal nests	75
Free Living Hosts	81

	Interactions of Argasid Ticks with the Wider Environment	84
III	MATERIALS AND METHODS	88
	Sites	88
	Burrows	89
	Sampling Technique	90
	Sorting	91
	Fluorescent Marking	93
	Temperature and Humidity Measurements	94
	Age and Sex Structure of Tick Populations	94
	Blood Meal Identification	94
	Invertebrate Identification	97
	Calculations and Statistics	99
IV	RESULTS AND DISCUSSION	100
	Animals Present at the Site	100
	Blood Meal Identification	109
	Host Preference	124
	Host Suitability for Population Growth	131
	Seasonality in Feeding and Population Growth	158
	Mortality	166
	Migration	169
	Survivorship	178
	Population Age Structure	181
	Trends in Population Growth	184
	Population Estimation	188
	Fisher-Ford estimate	188
	Removal estimate	189
	Biological Observations on Other Associated	
	Invertebrates	198
	Burrow Commensals	198
	Invertebrate parasites	217
	Invertebrate predators	227
	Dung decomposers	231
	General decomposers	233
V	CONCLUSION	238
	REFERENCES	244
	BIOGRAPHICAL SKETCH	278

LIST OF TABLES

Table	Page
2-1. A species list of the family Argasidae and the hosts they parasitize.	17
4-1. Vertebrates that are known to utilize the burrows constructed by gopher tortoises at the two sites.	101
4-2. Summary of results of the blood meal analyses on field collect <u>Ornithodoros t. americanus</u> at the Lochloosa flatwoods site.	110
4-3. Summary of results of the blood meal analyses on field collect <u>Ornithodoros t. americanus</u> at the Robert's ranch sandhill site.	111
4-4. Student's t-test comparisons of percentages of the <u>Ornithodoros t. americanus</u> populations fed in burrows in which either tortoise, frog or tortoise and frog served as host.	129
4-5. Student's t-test comparisons of differences between sequential population samples of <u>Ornithodoros t. americanus</u> larvae in which one sample did not have any fed ticks present. . . .	133
4-6. Student's t-test comparisons of differences between sequential population samples of <u>Ornithodoros t. americanus</u> first nymphs in which one sample did not have any fed ticks present. .	134
4-7. Student's t-test comparisons of differences between sequential population samples of <u>Ornithodoros t. americanus</u> second nymphs in which one sample did not have any fed ticks present. .	135
4-8. Student's t-test comparisons of differences between sequential population samples of <u>Ornithodoros t. americanus</u> third nymphs in which one sample did not have any fed ticks present. .	136
4-9. Student's t-test comparisons of differences between sequential population samples of <u>Ornithodoros t. americanus</u> late nymphs in which one sample did not have any fed ticks present. .	137

4-10.	Student's t-test comparisons of differences between sequential population samples of <u>Ornithodoros t. americanus</u> adults in which one sample did not have any fed ticks present. . . .	139
4-11.	Student's t-test comparisons of differences between larval and first nymphal numbers in sequential population samples of <u>Ornithodoros t. americanus</u> in which one sample did not have any fed ticks.	142
4-12.	Student's t-test comparisons of differences between first and second nymphal numbers in sequential population samples of <u>Ornithodoros t. americanus</u> in which one sample did not have any fed ticks.	143
4-13.	Student's t-test comparisons of differences between second and third nymphal numbers in sequential population samples of <u>Ornithodoros t. americanus</u> in which one sample did not have any fed ticks.	144
4-14.	Student's t-test comparisons of differences between third and late nymphal numbers in sequential population samples of <u>Ornithodoros t. americanus</u> in which one sample did not have any fed ticks.	145
4-15.	Student's t-test comparisons of differences between late nymphal and adult numbers in sequential population samples of <u>Ornithodoros t. americanus</u> in which one sample did not have any fed ticks.	146
4-16.	Student's t-test comparisons of differences between sequential population samples of <u>Ornithodoros t. americanus</u> larvae in which both samples had fed ticks.	147
4-17.	Student's t-test comparisons of differences between sequential population samples of <u>Ornithodoros t. americanus</u> first nymphs in which both samples had fed ticks.	148
4-18.	Student's t-test comparisons of differences between sequential population samples of <u>Ornithodoros t. americanus</u> second nymphs in which both samples had fed ticks.	149

4-19.	Student's t-test comparisons of differences between sequential population samples of <u>Ornithodoros t. americanus</u> third nymphs in which both samples had fed ticks.	150
4-20.	Student's t-test comparisons of differences between sequential population samples of <u>Ornithodoros t. americanus</u> late nymphs in which both samples had fed ticks.	151
4-21.	Student's t-test comparisons of differences between sequential population samples of <u>Ornithodoros t. americanus</u> adults in which both samples had fed ticks.	152
4-22.	Student's t-test comparisons of differences between larval and first nymphal numbers in sequential population samples of <u>Ornithodoros t. americanus</u> in which both samples had fed ticks. .	153
4-23.	Student's t-test comparisons of differences between first and second nymphal numbers in sequential population samples of <u>Ornithodoros t. americanus</u> in which both samples had fed ticks. .	154
4-24.	Student's t-test comparisons of differences between second and third nymphal numbers in sequential population samples of <u>Ornithodoros t. americanus</u> in which both samples had fed ticks. .	155
4-25.	Student's t-test comparisons of differences between third and late nymphal numbers in sequential population samples of <u>Ornithodoros t. americanus</u> in which both samples had fed ticks. .	156
4-26.	Student's t-test comparisons of differences between late nymphal and adult numbers in sequential population samples of <u>Ornithodoros t. americanus</u> in which both samples had fed ticks. .	157
4-27.	Seasonal feeding behavior of <u>Ornithodoros t. americanus</u> on hosts that inhabited gopher tortoise burrows at the Lochloosa site during 1984 and 1985.	159
4-28.	Seasonal feeding behavior of <u>Ornithodoros t. americanus</u> on hosts that inhabited gopher tortoise burrows at the Robert's ranch site during 1984 and 1985.	160

4-29.	Variation in the number of <u>Ornithodoros t. americanus</u> collected from gopher tortoise burrows in which a percentage had fed on an identifiable host.	167
4-30.	Longevity of <u>Ornithodoros t. americanus</u> under field conditions (observation period: 472-494 days).	179
4-31.	Removal sampling population estimates of <u>Ornithodoros t. americanus</u> in gopher tortoise burrows sampled at the Robert's ranch sandhill site.	191
4-32.	Removal sampling population estimates of <u>Ornithodoros t. americanus</u> in gopher tortoise burrows sampled at the Lochloosa flatwoods site.	193
4-33.	Population variation in removal estimates of <u>Ornithodoros t. americanus</u> in gopher tortoise burrows at the Robert's ranch sandhill site and at the Lochloosa flatwoods site between collection periods.	194
4-34.	Invertebrates collected in gopher tortoise burrows at the Robert's ranch sandhill site and at the Lochloosa flatwoods site. Month of collection and its association with the burrow are also included.	199
4-35.	Annual changes in the number of invertebrate species present in gopher tortoise burrows and the percentage soil water at the Robert's ranch sandhill location	218
4-36.	Annual changes in the number of invertebrate species present in gopher tortoise burrows and the percentage soil water at the Lochloosa flatwoods site	219

LIST OF FIGURES

Figure	Page
4-1. Blood meal analyses of fed <u>Ornithodoros t. americanus</u> at the Lochloosa pine flatwoods site. Percentages that each host contributed to the total number of meals analyzed for each stage	113
4-2. Blood meal analyses of fed <u>Ornithodoros t. americanus</u> at the Robert's ranch sandhill site. Percentages that each host contributed to the total number of meals analyzed for each stage	115
4-3. Seasonal feeding behavior of <u>Ornithodoros t. americanus</u> on hosts that inhabited gopher tortoise burrows, expressed as percentages of total burrows that had feeding occurring during the 1984-1985 sampling periods at the Lochloosa pine flatwoods site	162
4-4. Seasonal feeding behavior of <u>Ornithodoros t. americanus</u> on hosts that inhabited gopher tortoise burrows, expressed as percentages of total burrows that had feeding occurring during the 1984-1985 sampling periods at the Robert's ranch sandhill site	164
4-5. Age structure of the field population of <u>Ornithodoros t. americanus</u> in the sandhill habitat	183
4-6. Age structure of the field population of <u>Ornithodoros t. americanus</u> in the pine flatwood habitat	183
4-7. Mean estimated population size per gopher tortoise burrow for <u>Ornithodoros t. americanus</u> during the 1984-1985 sampling period at both the Lochloosa flatwoods and the Robert's ranch sandhill sites. (Correction factors applied to removal sampling estimates (Carle and Maughan, 1980).)	197
4-8. Cross sectional diagram of a typical gopher tortoise burrow with the locations where some commensal invertebrates are found	221

Abstract of Dissertation Presented to the Graduate
School of the University of Florida in Partial Fulfillment
of the Requirements for the Degree of Doctor of Philosophy

BIONOMICS AND ECOLOGY OF Ornithodoros (P.) turicata
americanus (MARX) (IXODOIDEA: ARGASIDAE)
AND OTHER COMMENSAL INVERTEBRATES PRESENT IN THE
BURROWS OF THE GOPHER TORTOISE, Gopherus polyphemus DAUDIN

By

ERIC GORDON MILSTREY

MAY 1987

Chairman: Jerry F. Butler

Major Department: Entomology and Nematology

The principal hosts of Ornithodoros (P.) turicata
americanus (Marx) are the gopher tortoise, Gopherus
polyphemus Daudin and the gopher frog, Rana areolata
aesopus Baird and Girard. Other hosts that were identified
or strongly implicated are the Southern toad, Bufo
terrestis (Bonnaterre), the Florida mouse, Peromyscus
(Podomys) floridanus Chapman, the opossum, Didelphis
virginiana (Kerr) and various snake species. Multiple host
feedings between molts were demonstrated in all life
stages. Implications for improved disease transmission and
reproductive potential were discussed. Although the
tortoise was the most common parasitized, the frog was the
preferred host. Both species could maintain the ticks but
the frog sustained greater population growth rates.

Population growth was maximized when both species concurrently served as tick hosts.

Larvae were the predominant age class collected (45.2%), the several stages of nymphs constituted 43.8% of the total with adults making up the remaining 11.0%. The male to female sex ratio was 2.3 to 1. Tick populations, calculated by removal sampling estimation, could be as high as 3300 but were more commonly below 200. Calculations using time survived in the field by individuals provides evidence that the life cycle of O. t. americanus could approach six years.

The major mortality factors for the soft tick species were desiccation due to low soil water content in the burrow or starvation due to the inability to locate a suitable host. The major mode of dispersion was concluded to be phoresy on the vertebrate hosts, but active dispersal could not be discounted.

Significant additions to the number of invertebrate species known to utilize the tortoise burrow were made. A number of new undescribed species were recovered. Year round biological observations provided new information on many of the commensals.

CHAPTER I
INTRODUCTION

The tick Ornithodoros (Pavlovskyella) turicata americanus (Marx) is found in peninsular Florida in the burrows of the gopher tortoise, Gopherus polyphemus (Daudin) and in some burrows occupied by burrowing owls, Athene cunicularia (Molina). The species, Ornithodoros turicata (Duges) is known from Mexico through the southwestern states of the United States to Kansas, with an allopatric population in Florida. Beck et al. (1986) resurrected americanus, the species' name given by Marx (1895) to this Florida tick population as a subspecific designation because of its distinctively different biology and ecology as compared to published records of the western strain. The taxonomic position of this Florida population is still uncertain because larval morphological characters can be used to distinguish the two strains (Milstrey, unpublished data) but biochemical tests, such as the gel electrophoresis technique used to separate Ornithodoros (P.) erraticus Lucas and O. (P.) sonrai Sautet and Witkowski (Wallis and Miller, 1983), have not yet been done. Research is in progress on cross breeding the subspecies (Telford, unpublished data). Further research in these areas may stabilize the taxonomic position of the species.

Since 1979 the Florida population of this soft tick or argasid has been extensively studied by Dr. J. F. Butler and his colleagues. A number of life history and behavioral studies have already been done (Beck et al., 1986, Wilkinson, unpublished data, Telford, unpublished data). The temperature preference of the subspecies was studied by Kilbourne (1981). The only field ecology done on the tick was undertaken by Adeyeye (1982). His studies concentrated on the interactions between the tick in the burrow and the outside environment. He found that ticks could be readily attracted out of the burrows to either a CO₂ source or an animal placed upon the burrow apron. He estimated tick populations to be between 47 and 1,338 in the burrows studied. Location within the burrow varied during the year with higher densities at the entrances in the summer and fall; the tick retreating deeper into the burrow in winter and spring.

The reason for the renewed interest in the study of this tick was due to a combination of two factors. The first was the introduction of African swine fever (ASF or ASFV) to the Caribbean and the possibility that this disease could invade the United States. The second was that native Ornithodoros ticks could transmit this agent (Groocock et al., 1980) and that, as in Spain, once

established in the native argasid tick population the virus might become endemic.

Florida is the gateway to the Caribbean for the United States. Gibbs and Butler (1984) summarized the risk factors for Florida being the "port of call" for ASF's entry into North America. Florida is the major stop off point for tourists going to, and illegal immigrants coming from, the islands of the Caribbean. Thousands of tons of cargo, both legal and illegal, worth millions of dollars, arrive on Florida's shores annually. Florida has a large population of both feral and domestic susceptible swine. Lastly, there are several Ornithodoros species present that could pick up the pathogen.

African swine fever is an arbovirus which has emerged as the single most important transmissible swine pathogen in the world. There are a number of important factors about this virus and the disease it causes that support this statement. A partial list of these factors include, the lack of a vaccine and no expectation for the imminent development of one, the virulence of the infection, carrier states in surviving swine, the ease of transmission, identification of the disease requiring multiple laboratory procedures utilizing immunofluorescent and cell culture techniques; and the existence of tolerant wild hosts and

Ornithodoros tick vectors (Hess, 1981; Wardley et al., 1983).

African swine fever virus is a member of the Iridovirus family. This family is characterized by having double stranded DNA with complex capsids formed in the cytoplasm (Andrewes et al., 1978). Most of these viruses infect invertebrates; some are found in lizards, fish and frogs but ASF is the only DNA virus classified as an arbovirus (Andrewes et al. 1978).

Montgomery, in 1910, first identified the disease in infected domestic pigs in Kenya (Montgomery, 1921). In those reported cases mortality rates were over 98%. For 40 years, cases were seen only in sub-Saharan Africa; then, in 1957 and 1960, cases were seen in Spain and Portugal (Wardley et al., 1983; Wilkinson, 1981). African swine fever became endemic on the Iberian peninsula and, since then, the virus has become a worldwide problem, spreading temporarily into Europe, the Mediterranean, South America and some Caribbean Islands (Gibbs 1981). Because of the lack of any other effective control strategy, the present method of disease control for this virus is total eradication of all diseased or exposed swine. African swine fever in Africa is also a sylvatic disease. There are three normal hosts for the virus: the warthog, Phacochoerus aethiopicus Pallas; bush pig, Potamochoerus

porcus (L.); and the giant forest hog, Hylocherus meinertzhageni Thomas. The virus appears to be transmitted normally by the bite of the soft tick that lives in the burrow, Ornithodoros (Ornithodoros) porcinus porcinus Walton. Other haematophagous arthropods present were not implicated in transmission (Plowright, 1975). In the warthog the infection is inapparent (Thomson et al., 1980).

Plowright found that in the tick Ornithodoros (O.) p. porcinus, the ingested virus replicates in the midgut of the tick and then invades the haemocoel and other tissues, including the reproductive organs. Once established in the tick it may be transmitted transtadially, venereally and transovarially (Plowright et al., 1970, 1974; Plowright, 1975, 1977). Thomson (1985) stated that Ornithodoros ticks remain attached to warthogs outside the burrow but may fall off later near pig sties, and that these ticks and not wild swine exposure are the source of virus in primary outbreaks of ASF in southern and East Africa.

One of the factors that contributed to the virus becoming endemic in the Iberian peninsula was that it became established in the local Ornithodoros (P.) maroccanus Velu (O. erraticus "large race") population through feeding on infected swine (Sanchez Botija, 1963). Four species, not involved with natural transmission cycles, have been shown to be able to pick up and transmit the virus under

laboratory conditions: Ornithodoros (O.) coriaceus Koch (Groocock et al., 1980), O.(P.) turicata americanus and O.(A.) puertoricensis Fox (Butler et al., 1984a), and O.(O.) savignyi (Audouin) (Mellor and Wilkinson, 1985).

Several biological facts about Ornithodoros ticks confound the potential for ASF disease control. First, is that they are very long lived, probably at least 10 years in favorable sites (Pavlovskii and Skrynnik, 1960). They are often inactive for years at a time and maintain themselves in locations that are inaccessible to normal methods of pesticide application such as burrows, under rocks or bushes and in cliff or cave niches. They do not stay on the host for long, thus minimizing pesticide exposure. Some species have larvae that attach to the host for about a week, providing a method for effective dispersion. Many Ornithodoros ticks have a diverse host range feeding on whatever is available--amphibian, reptile, bird or mammal, rarely dependent upon a single host. Thus, if the local tick species becomes infected with the ASF virus, we will be unable to eradicate it from the habitat or protect the stock by direct pesticide application (Hoogstraal, 1956), and it may be several years before it is evident that the ticks are infected because of aestivation or delay in an infected tick coming into contact with a pig.

Recently, several methods have been developed that can be used to identify infections in Ornithodoros ticks. Geering et al. (1986) developed the immunodot blot test for detecting ASFV antigens in the hemolymph of Ornithodoros coriaceus. It has promising field applications for detecting ASFV and other tick-borne pathogens. Besides the immunodot blot test, Endris et al. (1986) also used the hemolymph test for direct immunofluorescence and virus culture in buffy coat cells to confirm the presence of ASFV in the tick. The notable advantages of the hemolymph test are that it can be used on individual ticks, that it does not kill the ticks and so they can therefore be used for further study.

Although ASF is an arbovirus, vector transmission is not the primary method of swine transmission outside Africa. Internationally, it appears that the major mode of transmission is from the ingestion of uncooked or cured pork products (Gibbs and Butler, 1984). Within a herd, the virus spreads swiftly by contact (Scott, 1965) or air (Wilkinson, 1981). It can also be transmitted by germ plasm (Gibbs, 1981) or mechanically from contaminated farms or veterinary tools. In the endemic areas of Spain and Africa, domestic and wild swine encounters must be guarded against. The ease of transmission is the primary difficulty encountered when attempting to control the

disease. Since the virus is relatively resistant and can survive on contaminated surfaces for at least 60 days (Endris and Hess, personal communication), personnel, equipment and vehicles moving between farms can readily transfer the virus between herds (Wardley et al., 1983).

The original African swine fever isolates of Montgomery (1921) were highly virulent. The high virulence of the African isolates has not been maintained with the disease's expansion outside Africa (Hess, 1981). These lower virulent strains have complicated the control of the disease for three reasons: (1) the development of higher numbers of inapparent swine carriers, (2) the less distinct symptoms that characterize the disease and (3) the development of nonhemadsorptive virus strains. Pigs may survive initial infection with little or no symptomology from these lower virulent strains but these chronic carriers can infect the whole herd before the disease is recognized (DeTray, 1957).

Disease recognition and confirmation is a difficult problem. African swine fever has the same symptoms as hog cholera and other hemorrhagic diseases (Wardley et al., 1983). Only in those herds that have had hog cholera vaccination and still come down with the symptoms is ASF likely to be suspected. Confirmation of the disease must be done in a laboratory using a combination of

immunofluorescent and cell culture techniques, but 1% still remain undetectable (Hess, 1981). Therefore, negative results do not always confirm the herd is disease free.

In order to protect Florida and the rest of the United States, this study was undertaken to better understand the argasid ticks that could serve as potential vectors before the introduction of ASF. The objectives of my study on O.(P.) t. americanus were to (1) identify the natural hosts of the tick, (2) identify the principal factors controlling the population dynamics in the burrow systems of the host gopher tortoise, and (3) to collect other invertebrate species which cohabit the burrow system and expand the information known about these species. Throughout the range of the gopher tortoise, tortoise populations are being threatened. Some states now consider them endangered and so the burrow's endemic fauna is threatened. Collection of these endemic invertebrates, therefore, provides (1) recognition of unknown species before they become extinct, (2) a data base to gauge the impact of decreased tortoise populations, and (3) an annual perspective of invertebrate populations since the three previous studies were short term (Hubbard, 1894, 1896; Young and Goff, 1939; Woodruff, 1982). Since this burrow habitat has been present since the early Pleistocene period (Auffenburg, 1969), an investigation of the fauna could

provide an unparalleled view of the past evolutionary history and stability of the commensal invertebrate community.

CHAPTER II
ARGASID NICHE SPECIALIZATION IN RELATION TO SYSTEMATICS
AND PATHOGEN TRANSMISSION

Historical Perspective: Ticks as Disease Agents

In order to evaluate the epidemiology of potential New World soft tick vectors of ASFV and other diseases, the interactions of known soft tick vectors, the diseases they transmit and their ecological habitats are reviewed. This review provides a worldwide perspective of both Ornithodoros and Argas tick problems. This broad view is required since modern transportation methods and ecological manipulation have enhanced the possibility that regional disease/vector problems can become international ones (Gibbs, 1981; Hoogstraal, 1985). Hard tick (Ixodidae) diseases and their transmission were not included with the exception of those diseases that have also been demonstrated in soft ticks.

The family Argasidae was largely ignored during the early years of tick research, other than the taxonomic work by Nuttall and Warburton (1908). In the 1930s, relapsing fevers were recognized as important soft tick transmitted diseases. Interest in the diseases was so strong that in 1941 an American Association for the Advancement of Science (AAAS) symposium was held on the subject because relapsing fever was "spreading in the United States, particularly in

the southern and western parts . . . and is widely prevalent in Latin America" (Moulton, 1942, P4). The study of this disease by Drs. G. E. Davis and E. Brumpt provided significant increases in the knowledge of the biology of the burrow and house inhabiting Ornithodoros vectors, as well as providing the research momentum to greatly increase the number of collected soft tick species. This served as the initiation point for the extensive study of argasid taxonomy by Cooley and Kohls in 1944. Since this time many more species have been described and the genera and subgenera have stabilized.

In the last 25 years, with the widening interest and improvements in the isolation and identification of arthropod transmitted viruses (arboviruses), interest in the Argasidae as disease vectors has renewed. In the same period, the "ecology movement", increased the awareness of wildlife and their diseases. These two factors undoubtedly provided the research interest necessary for the increased number of examinations of zoonoses involving wild animals and their parasites, including argasids. These studies increased the number of viruses and tick species known.

Classification of the Ixodoidea

Morphology

An important part of any study comparing the host and habitat specificity of an arthropod is the ability to identify the arthropod in question. Not only must an arthropod species be identifiable, but separable from other similar species. Additionally, the taxonomic study of those other related species provides (1) a point of reference for the study of those other related species, (2) a view of the evolutionary variety in the group and the phylogeny of the species and (3) host and habitat specificity of the group. Comparison of the phylogeny, physiology and specificity of the related species may provide data in aiding inference on the ecology and possibly the evolutionary history of the species under study.

Ticks are classified in the order Metastigmata or Parasitiformes depending on the systematist consulted (Kranz, 1978). The superfamily Ixodoidea Banks contains all three tick families: Argasidae, Ixodidae and Nuttalliellidae. Argasidae are leathery with no scutum, and the fourth palpal segment is apical. In the other two families a scutum is present on all stages. In the Nuttalliellidae the scutum and integumental texture is similar and the fourth palpal digit is apical. The

Ixodidae, or hard ticks, have a scutum which is strongly sclerotized and distinct from the integument, and the fourth palpal digit is reduced and arises from a subterminal ventral pit on the third segment (Hoogstraal, 1973a).

Developmental and Behavioral Characteristics

Argasids have specialized in feeding for short periods of time on hosts that intermittently visit the site where the ticks are present. These ticks are normally found in arid locations or in areas where there are long dry seasons. In areas with heavy rainfall they are restricted to caves, treeholes or dry crevices, rarely burrows (Hoogstraal, 1973a). The short host exposure time, limited habitats, long survival time away from the host and strong thigmotropic response of these ticks have contributed to their being so poorly known.

The biologically more diverse family Ixodidae is much better known due to its parasitic behavior. It is active on the soil and vegetation questing for hosts, where it feeds for long periods and on which it mates. The family also has many species that parasitize man's livestock and other animals he utilizes.

Besides the behavioral differences between argasids and ixodids there are some important physiological

differences. Ixodids have only one nymphal stage whereas argasids have two to eight (Hoogstraal, 1973a). In the Argasidae some species have non-feeding stages, either as larvae or first nymphal stage. Argasids mate off the host. In the ixodids, females lay one large egg batch, numbering up to 20,000, and then die. Argasid females lay many egg batches before they die, usually with a blood meal preceding each. Argasid egg batches are much smaller, numbering in the hundreds.

The family Nuttalliellidae is represented by one African species: Nuttalliella namagua Bedford. It is known only from 21 specimens collected from host animal skins, from under rocks and in swallow nests (Keirans et al., 1976; Hoogstraal, 1985). Hoogstraal (1985) stated that the major host is probably the rock hyrax.

Besides Bedford's (1931) description and the redescription of Keirans et al. (1976) using scanning electron microscopy, two other investigations have been done. Roshdy et al. (1983) studied spiracle structure and El Shoura et al. (1984) studied female internal morphology. They found certain characters similar to either argasids or ixodids and some unique structures. The internal and external distinctiveness of Nuttalliella led El Shoura et al. (1984) to conclude that it represents a phylogenetically distinct branch derived from the prototype

Ixodoidea base and is not the missing link between argasids and ixodids.

Systematics of Argasidae

The family Argasidae is split into five genera: Argas, Ornithodoros, Otobius, Antricola and Nothoaspis. Each genus also is in its own subfamily but, except for Argas, the rest of the genera are thought to be derived from Ornithidorine stock (Hoogstraal, 1985). However most authors consider the last four genera to be in the subfamily Ornithodorinae. A list of the species present in the family and their hosts is presented in Table 2-1. The list is presented in alphabetic order within each group or subgenus as the phylogenetic relationships for most of the species are unclear. This classification is not the only one--the Russian, Pospelova-Shtrom in 1946 and 1969 proposed another scheme. Notable points in it are the generic resurrection of Carios (Argas subgenus), Alveonasus (Ornithodoros subgenus) and Alectrobius (Ornithodoros subgenus) and the development of three tribes. In the tribe Otobiini, Otobius and Alveonasus are separated from the other Ornithidorinae based primarily upon the similarities in feeding and development of some of the species present in both genera. Although both systems have their strengths and weaknesses (Pospelova-Shtrom, 1969),

Table 2-1. A species list of the family Argasidae and the hosts they parasitize.^a

Family Argasidae Canestrini 1890	
Subfamily Argasidinae	
Genus <u>Argas</u> Latreille 1796	
Subgenus <u>Argas</u> Latreille 1796	
"reflexus group"	pigeon
<u>africolumbae</u> Hoogstraal, Kaiser, Walker, Ledger and Converse 1975	pigeon
<u>beijingensis</u> Teng 1983	owl, falcon, wren, woodpecker
<u>brevipex</u> Banks 1905	burrowing owl
<u>dalei</u> Clifford, Keirana, Hoogstraal and Corwin 1976	pigeon
<u>hermanni</u> Audouin 1827	snow partridge
<u>himalayensis</u> Hoogstraal and Kaiser 1972	pigeon, swallow
<u>latus</u> Filippova 1961	cormorant
<u>macrostigmatus</u> Filippova 1961	pigeon
<u>polonicus</u> Siuda, Hoogstraal, Clifford and Wassef 1964	pigeon
<u>reflexus</u> (Fabricius 1794)	sparrow, pigeon
<u>tridentatus</u> Filippova 1961	pigeon, sparrow, owl, crow, falcon
<u>vulgarus</u> Filippova 1961	-----
(A.) sp. Egypt origin (Clifford et al. 1983 *)	
"japonicus group"	swallow
<u>assimilis</u> Teng and Song 1983	swallow
<u>cooleyi</u> Kohls and Hoogstraal 1960	gull
sp. near <u>cooleyi</u> Hoogstraal 1985*	falcon
<u>falco</u> Kaiser and Hoogstraal 1973	swallow
<u>japonicus</u> Ysmaguti, Clifford and Tipton 1968	faity martin
<u>lagenoplastis</u> Froggatt 1906	falcon
<u>lowryae</u> Kaiser and Hoogstraal 1975	

Table 2-1. (cont.)

"monachus group"		palm chat
dulus Keirans, Hoogstraal and Capriles 1971		monk parakeet
monachus Keirans, Radovski and Clifford 1973		
"neghnei group"		pigeon, chicken, man
neghmei Kohls and Hoogstraal 1961		chicken, wild birds, man
moreli Keirans, Hoogstraal and Clifford 1978		
"cucumerinus group"		vulture, pelican
cucumerinus Neumann 1901		pigeon, chicken
magnus Neumann 1896		
Subgenus <u>Persicargas</u> Kaiser, Hoogstraal and Kohls 1964		
"persicargas group"		chicken, arboreal nesting birds
persicus (Oken 1818)		dove
steptopelia Hoogstraal, Kaiser and Kohls 1968		
"arboreus group"		heron
arboreus Kaiser, Hoogstraal and Kohls 1964		chicken, small birds
miniatus Koch 1844		crow
nullarbornensis Hoogstraal and Kaiser 1973		heron, stork, cormorant
robertsi Hoogstraal, Kaiser and Kohls 1968		chicken, dove, quail, turkey
sanchezi Duges 1891		chicken
walkerae Kaiser and Hoogstraal 1969		-----
(p.) sp. Madagascar origin (Hoogstraal et al. 1983 *)		
"giganteus group"		ground nesting birds
giganteus Kohls and Clifford 1968		
"beklemischevi group"		vulture
abdussalami Hoogstraal and McCarthy 1965		vulture
beklemischevi Popelova-Shtrom, Vasilyeva and Semashko 1961		vulture, turkey, chicken
radiatus Railliet 1893		vulture
ricci Hoogstraal, Kaiser, Clifford and Keirans 1975		vulture
thellerae Hoogstraal and Kaiser 1970		

Table 2-1. (cont.)

<u>zumpti</u> Hoogstraal, Kaiser and Kohls 1968	vulture
"ungrouped Pernicargan species" (p.) sp. South African origin (Hoogstraal 1985 *)	
Subgenus <u>Microargas</u> Hoogstraal and Kohls 1966	
<u>transveranus</u> Banks 1902	Galapagos tortoise
Subgenus <u>Carios</u> Latreille 1966	
<u>australiensis</u> Kohls and Hoogstraal 1974	insectivorous bats
<u>daviesi</u> Kaiser and Hoogstraal 1973	insectivorous bats
<u>dewse</u> Kaiser and Hoogstraal 1974	insectivorous bats
<u>macrodentus</u> Hoogstraal, Moorhouse, Wolf and Wassef 1977	insectivorous bats
<u>pusillus</u> Kohls 1950	insectivorous bats
<u>sinensis</u> Jev and Zhu 1982	insectivorous bats
<u>vespertilionis</u> (Latreille 1802)	insectivorous bats
Subgenus <u>Chiropterargas</u> Hoogstraal 1955	
<u>boueti</u> Roubaud and Colas-Belecour 1933	insectivorous bats
<u>confusus</u> Hoogstraal 1955	insectivorous bats
<u>cordiformis</u> Hoogstraal and Kohls 1967	insectivorous bats
<u>cylonicensis</u> Hoogstraal and Kaiser 1968	insectivorous bats
Subgenus <u>Secretargas</u> Hoogstraal 1957	
<u>echinops</u> Hoogstraal, Uilenberg and Blanc 1967	hedgehog
<u>hoogstraali</u> Morel and Vassiliades 1965	lizards
<u>transgargiepims</u> (White 1846)	insectivorous bats
Subgenus <u>Ogadenus</u> Fospelova-Shtrom 1946	
<u>brumpti</u> Neumann 1907	rock hyrax, lizarda, birds

Table 2-1. (cont.)

Ungrouped Argas species

brueschi Dryanski 1957
sp. Afghanistan origin (Hoogstraal et al., 1979 *)

Subfamily Ornithodorinae

Genus Ornithodoros Koch 1844

Subgenus Ornithodoros Koch 1844

apertus Walton 1962
compactus Walton 1962
eremicus Cooley and Kohls 1941
indica Rau and Rao 1971
moubata (Murray 1877)
porcinus Walton 1962
procaviae Theodor and Costa 1960
savignyi (Audouin 1827)

Subgenus Pavlovskyella Pospelova-Shtrum 1950

alactagalis Issakjan 1936
arenicolous Hoogstraal 1953
asperus Warburton 1918 (= verrucosus)
braziliensis Aragao 1923
cholodkovski Pavlovsky 1930
erraticus (Lucas 1849)
foleyi Parrot 1928 (=francheri)
furcosus Neumann 1908
graingeri Heish and Guggisberg 1953
grenieri Klein 1964
gurneyi Warburton 1926
hermsi Wheeler, Herms and Meyer 1935
macmillani Hoogstraal and Kohls 1966

Citellus sp.
lizards

porcupine, warthog
tortoises
deer mice
barking deer
warthog, porcupine, man
warthog, porcupine, man
rock hyrax
camel, man

rat, hamster, badger, lizards
rodents, hedgehog, lizards
rodents, hedgehog, lizards
goat, tortoise, lizards, snake
mammals, man, birds
bats
hedgehog, rodents, lizards, toad
domestic livestock, man
porcupine, bat, man
rodent (Hypogeomys)
kangaroo
chipmunk, mice, bat, bird, squirrel
cockatoo, owl

Table 2-1. (cont.)

<u>maroccanus</u> Velu 1919	swine, rodents, rabbit
<u>nerensis</u> Pavlovsky 1941	burrowing mammals
<u>nicolleti</u> Mosser 1932	<u>Neotoma</u> , dog, squirrel, man
<u>normandi</u> Larrousse 1923	rodents
<u>parkeri</u> Cooley 1936	prairie dogs, <u>Citellus</u> , burrowing owls
<u>rostratus</u> Arago 1911	burrowing rodents, dog, man, peccary
<u>sonrai</u> Sautet and Witkowski 1944	<u>Mastomys</u> , grass rat (<u>Arsicanthis</u>)
<u>sparsus</u> Kohls and Clifford 1963	<u>Peromyscus</u> , <u>Neotoma</u>
<u>tartakowski</u> Olenov 1931	rodents, carnivores, tortoise
<u>tholozani</u> Laboulbene and Megnin 1882	man, sheep, hedgehog, rodent
<u>turicata</u> (Duges 1876)	tortoise, snake, burrowing owls, pig,
<u>verrucosus</u> Olenov, Zasukhin and Fenyuk 1934	<u>Citellus</u> , <u>Neotoma</u> , man
<u>zumpti</u> Heisch and Gugginberg 1953	burrowing rodents
Subgenus <u>Ornamentum</u> Clifford, Kohls and Sonenshine 1964	rat, mouse
<u>coriacens</u> Koch 1844	deer, cattle, man
Subgenus <u>Alectrobius</u> Pocock 1907	
"bat feeding group"	
<u>asteci</u> Matheson 1935	insectivorous bats
<u>basei</u> (Schulze 1935)	insectivorous bats
<u>bolivensis</u> Kohls and Clifford 1964	insectivorous bats
<u>brodyi</u> Matheson 1935	insectivorous bats
<u>clarki</u> Jones and Clifford 1972	insectivorous bats
<u>dusabeki</u> Cerny 1967	insectivorous bats
<u>dyeri</u> Cooley and Kohls 1940	insectivorous bats
<u>eptenicus</u> Kohls, Clifford and Jones 1969	insectivorous bats
<u>basei</u> Schulze 1940 (= <u>dunni</u>)	insectivorous bats
<u>jul</u> Schulze 1940	insectivorous bats
<u>kelleyi</u> Cooley and Kohls 1940	insectivorous bats
<u>knoxjonesi</u> Jones and Clifford 1972	insectivorous bats
<u>mimon</u> Kohls, Clifford and Jones 1969	insectivorous bats
<u>peropteryx</u> Kohls, Clifford and Jones 1969	insectivorous bats

Table 2-1. (cont.)

peruvianus Kohls, Clifford and Jones 1969	insectivorous bats
rossi Kohls, Sonenshine and Clifford 1965	insectivorous bats
setonus Kohls, Clifford and Jones 1969	insectivorous bats
stageri Cooley and Kohls 1941	insectivorous bats
tagaridae Cerny and Dusbabek 1967	insectivorous bats
tiptoni Jones and Clifford 1972	insectivorous bats
ymatensis Cooley and Kohls 1940	insectivorous bats
"capensis group - bird parasites"	
ambulus Chamberlin 1920	cormorant, pelican, booby, tern
capensis Newmann 1901	penguin, gull, tern
collocaliae Hoogstraal, Kadarasan, Kaiser and VanPeenen 1974	cave swiftlets
coniceps Canistrini 1890	pigeon
denmarki Kohls, Sonenshine and Clifford 1965	tern, gull, booby
sp. near denmarki California origin (Clifford, 1979 *)	various marine birds
maritimus Vermeil and Marguet 1967	gull, tern
muesbecki Hoogstraal 1969	booby
swaili Kitaoka and Suzuki 1973	shearwaters
spheniscus Hoogstraal, Wassef, Hays and Keirans 1985	penguin
yunkerii Keirans, Clifford and Hoogstraal 1984	tern, booby, albatross, penguin
"Galapagos iguana group"	
darwini Kohls, Clifford and Hoogstraal 1980	iguana
galapagensis Kohls, Clifford and Hoogstraal 1980	iguana
"miscellaneous host group"	
casebeerii Jones and Clifford 1972	rodent (<u>Orthylomys</u>)
chironectes Jones and Clifford 1972	marsupial (<u>Chironectes</u>), cotton rat
concanensis Cooley and Kohls 1941	bat, swallow, raptor
cycluriae de la Cruz 1984	iguana
echinys Kohls, Clifford and Jones 1969	rodent (<u>Echinys</u>), marsupial (<u>Marmosa</u>)
marmosae Jones and Clifford 1972	marsupial (<u>Marmosa</u>)
puertoricensis Fox 1947	rat, rabbit
talaje (Guertin-Meneville 1849)	Neotoma, man, dog, cat, chicken
tuttlei Jones and Clifford 1972	tapir, <u>Agouti</u>

Table 2-1. (cont.)

<u>Subgenus Protnekalia</u> Keirans, Hoogstraal and Clifford 1977	
<u>peringueyi</u> Bedford and Hewitt 1925	swallow
<u>peusi</u> (Schulze 1943)	swallow
<u>vansomerini</u> Keirans, Hoogstraal and Clifford 1977	swallow
<u>Subgenus Subparmatius</u> Clifford Kohls and Sonenshine 1964	
<u>marinkellei</u> Kohls, Clifford and Jones 1969	insectivorous bats
<u>mormoepi</u> Kohls, Clifford and Jones 1969	insectivorous bats
<u>viguierani</u> Cooley and Kohls 1941	insectivorous bats
<u>Subgenus Alevonasmus</u> Schulze 1944	
<u>acinus</u> Whittick 1938	large mammals
<u>canestrinii</u> (Birula 1895)	sheep, cattle
<u>delancoeli</u> Roubaud and Collas-Belcour 1931	hedgehog
<u>ehorisi</u> Theiler 1959	porcupine
<u>foleyi</u> Parrot 1928	sheep, antelope, gerbil, man
<u>lahorensis</u> Newmann 1908	domestic livestock, mouflon
<u>Subgenus Reticulinasmus</u> Schulze 1941	
<u>batuensis</u> Hirst 1929	fruit bats
<u>chiropterphila</u> Dhandu and Rajagopalan 1971	fruit bats
<u>fauni</u> Hoogstraal 1960	fruit bats
<u>madagascariensis</u> Hoogstraal 1962	fruit bats
<u>rennelliensis</u> Clifford and Sonenshine 1962	fruit bats
<u>salahi</u> Hoogstraal 1953	fruit bats
<u>solomonis</u> Dumbleton 1958	fruit bats
<u>steinii</u> (Schulze 1935)	fruit bats
<u>sp. New Guinea origin</u> (Hoogstraal, 1985 *)	fruit bats
<u>sp. New Guinea origin</u> (Hoogstraal, 1985 *)	fruit bats
<u>sp. Thailand origin</u> (Hoogstraal, 1985 *)	fruit bats

Table 2-1. (cont.)

Ungrouped Ornithodoros species

<u>aragasi</u> Fonseca 1960	<u>Oryzomys "rat"</u>
<u>cooley</u> McIntosh 1935	<u>carnivores</u>
<u>davisi</u> Fonseca 1960	<u>Oryzomys "rat"</u>
<u>elongatus</u> Kohls, Clifford and Sonenshine 1965	<u>iguana</u>
<u>natalinus</u> Cerny and Dusbabek 1967	<u>insectivorous bats</u>
<u>nattereri</u> Warburton 1927	<u>host unknown</u>
<u>rudis</u> Karsch 1980 (= <u>venezuelensis</u>)	<u>man, rodents, chicken</u>
Genus <u>Otobius</u> Banks 1912	
<u>lagophilus</u> Cooley and Kohls 1940	<u>rabbit, hare</u>
<u>magnini</u> (Duges 1884)	<u>deer, antelope, cattle</u>
Genus <u>Antricola</u> Cooley and Kohls 1942	
Subgenus <u>Antricola</u> Cooley and Kohls 1942	
<u>cernyi</u> de la Cruz 1978	<u>insectivorous bats</u>
<u>coprophilus</u> McIntosh 1935	<u>insectivorous bats</u>
<u>habensis</u> de la Cruz 1976	<u>insectivorous bats</u>
<u>martelorum</u> de la Cruz 1978	<u>insectivorous bats</u>
<u>mexicanus</u> Hoffman 1959	<u>insectivorous bats</u>
<u>noemiae</u> de la Cruz 1978	<u>insectivorous bats</u>
<u>occidentalis</u> de la Cruz 1978	<u>insectivorous bats</u>
<u>silvai</u> Cerny 1967	<u>insectivorous bats</u>

Table 2-1. (cont.)

Subgenus Parantricola Cerny 1966marginatus (Banks 1910)

insectivorous bats

Genus Nothosaspis Keirans and Clifford 1975reddelli Keirans and Clifford 1975

insectivorous bats

a : Compiled from de la Cruz, 1978a; Hoogstraal, 1985; Hoogstraal et al., 1979b; Jones and Clifford, 1972; Kohls et al., 1965 and Sonenshine et al., 1966.

* : The reference in which the existence of the undescribed species is mentioned.

the American system used in this paper is utilized by most of the world's acarologists.

Genus: Argas

The genus Argas has 56 species recognized at this time. They are grouped into seven subgenera and numerous subgroups (Hoogstraal et al., 1979b). Definitions of the subgenera are found in several publications: A. (Argas), (Hoogstraal, 1957); A. (Persicargas), (Kaiser et al., 1964); A. (Ogadenus), (Pospelova-Shtrom, 1946); A. (Chiropterargas), (Hoogstraal, 1955); A. (Carios), (Hoogstraal, 1958); A. (Secretargas), (Hoogstraal, 1957); and A. (Microargas), (Hoogstraal and Kohls, 1966b). Other references that should be consulted for systematic separation are Sonenshine et al. (1962) for larval characters and four papers on differences in the structure of the Haller's organ in the genus Argas; Clifford et al. (1983), Hoogstraal et al. (1983), Hoogstraal et al. (1984) and Roshdy et al. (1984). Ecologically all Argas species are restricted to dry niches in desert, semi-desert, steppe or savanna environments with long dry seasons or dry caves and shelters. The one exception is A. (A.) macrostigmatus Filippova which parasitizes crested cormorants, Phalacrocorax aristotelis L., on islands in the Black Sea (Hoogstraal et al., 1979b).

The subgenus Argas has 25 species, distributed worldwide (Hoogstraal et al., 1979b; Hoogstraal, 1985). All members of the subgenus Argas parasitize birds. Most parasitize birds on rocky nest sites such as cliffs, rocky islands or stone masonry; the exceptions are the arboreal nest parasites: A. dulus Keirans, Hoogstraal and Capriles on the palm chat, Dulus dominicus (L.), in the Dominican Republic (Keirans et al., 1971), A. monachus Keirans, Radovski and Clifford on monk parakeets, Myiopsitta monachus (Boddaert) in Argentina (Keirans et al., 1973), and A. brevipes Banks which is found in tree holes and parasitizes the birds that nest in these shelters (Kohls et al., 1961). The Neotropical A. dalei Clifford, Keirans, Hoogstraal and Corwin parasitizes the burrows of the South American variety of the burrowing owl Athene cunicularia (Clifford et al., 1976). There are two species of the subgenus; A. (A.) cucumerinus Neumann and A. (A.) macrostigmatus that specialize in parasitizing marine birds (Hoogstraal, 1985).

The subgenus Persicargas consists of 15 species distributed worldwide (Hoogstraal et al., 1979b). All species in this subgenus parasitize birds that return annually to the same nesting or resting site, or that remain at the same site year round. All but one species inhabits trees (Hoogstraal et al., 1983). The exception,

A.(P.) zumpti Hoogstraal, Kaiser and Kohls is found in vulture nests in rocky situations but Hoogstraal (1985) suspects it also inhabits trees.

The subgenus Microargas has only a single representative species, Argas (M.) transversus Banks, a parasite of the several subspecies of the Galapagos tortoise, Geochelone elephantopus (Harlan) (Hoogstraal et al., 1973). This very small tick (1.5 x 2.3 mm) undergoes its entire life cycle, including the egg stage, under the carapace of the tortoise against the leathery skin.

The subgenus Carios is composed of six bat parasitizing species, one in the Palearctic, Ethiopian and Oriental regions, two in the Oriental region and the rest in the Australian region (Hoogstraal et al., 1979b; Hoogstraal, 1985).

The subgenus Chiropterargas consists of four Old World species. The hosts for these ticks are a wide variety of genera of insectivorous bats (Hoogstraal, 1985).

The subgenera Carios and Chiropterargas have branched from a single stem which apparently evolved from an Argas parasite of birds nesting among rocks and adapted to cave-dwelling bats (Roshdy et al., 1984). Roshdy et al. (1984) summarized the external morphological similarities of the two subgenera and focused on the Haller's organ structure. In both subgenera the Haller's organ roof is solid,

differing from Argas, Microargas and Secretargas. The Chiropterargas, in the evolutionary process, have diverged more than Carlos from the typical Argas (Hoogstraal, 1985).

The subgenus Secretargas consists of three species, a single African species and two from Madagascar. Roshdy (1963) examined the internal morphology of A.(S.) transgaripepinus and agreed with Hoogstraal's (1957) conclusion that the subgenera Argas and Secretargas are closely related.

The subgenus Ogadenus has only one species, Argas O. brumpti Neumann, found in the eastern and southern portion of the Ethiopian region.

In the Haller's organ study of Hoogstraal et al. (1984) on Secretargas and Ogadenus a number of evolutionary conclusions and hypotheses were presented. The Malagasy Secretargas species and A.(O.) brumpti parallel some Ornithodoros evolutionary trends such as sheltering in soil, lizard host specificity and the phylogenetically primitive unroofed Haller's organ capsule, but retain the lateral suture that characterizes the Argas-Persicargas stem of the genus Argas from which they evolved.

Genus: Ornithodoros

The genus Ornithodoros consists of about 110 species in eight subgenera. However several species are unplaced

in any subgenera. Presently accepted subgeneric classification was developed by Clifford et al. (1964) and expanded by Keirans et al. (1977a). Taxonomic position within subgenera, however, is not as well developed as for Argas. Classification in the genus is heavily dependent upon larval characteristics and is seen in the series of papers describing most of the world's known larvae: Western Hemisphere larvae (Kohls et al., 1965), Eastern Hemisphere larvae (Sonenshine et al., 1966) and two revisions to include fifteen new Western Hemisphere species (Kohls et al., 1969; Jones and Clifford, 1972). Filippova (1966) gives a comprehensive review of the Soviets' argasid fauna. Hoogstraal (1985) has summarized most subsequent information.

The subgenus Ornithodoros has eight representative species. Most species are present in the Ethiopian region with the O.(O.) moubata complex and O.(O.) savignyi, but the Nearctic has O.(O.) eremicus Cooley and Kohls, the Oriental region has O.(O.) indica Rau and Rao, and the Palearctic O.(O.) procaviae Theodor and Costa (Hoogstraal, 1985).

The sub-Saharan O.(O.) moubata superspecies was split by Walton (1962). His classification includes O.(O.) apertus Walton, associated with African porcupines, Hystrix; O.(O.) compactus Walton, associated with several

tortoise species, Testudo, south of the Zambezi river; domestic and wild races of O.(O.) moubata (Murray) and two subspecies of O.(O.) porcinus Walton: porcinus a wild strain associated with warthogs, Phacochoerus, and domesticus found in East African dwellings. Because of the recent species split, much of the published literature on O.(O.) moubata is difficult to interpret as to which species or subspecies is being discussed. Several papers by Walton (1953, 1957, 1958, 1960, 1964, 1979) could aid in this interpretation.

The subgenus Pavlovskyella has 32 species that occur in all regions of the world (Hoogstraal, 1985). All species are primarily restricted to caves, burrows or dens. All but one species parasitize mammals. However many are known to utilize birds (4 species) and reptiles (5 species) as blood sources also (Hoogstraal, 1985).

The subgenus Ornamentum is represented only by the pajaroello, O.(O.) coriaceus Koch, a Nearctic species found on the Pacific slope from California to Mexico. The species parasitizes large herbivores, including deer and cattle, and occasionally man. It is found in the soil under trees that serve as "deer beds" in scrub oak forests (Cooley and Kohls, 1944). This species is unique in that it possesses two pairs of two eyes.

The subgenus Alectorobius is the largest in the genus and the most diverse in habitat and host preference. It is primarily a New World subgenus with a few Old World species related to the marine bird parasite, O.(A.) capensis Neumann. Hosts of the subgenus are bats (20 species), birds (11 species), Galapagos iguanid lizards (2 species) or miscellaneous hosts (9 species) (Hoogstraal, 1985).

The subgenus Proknekalia consists of three rare swallow (Hirundo spp.) parasitizing species from the Palearctic and Ethiopian regions. The subgenus is closely related to Alveonasus and is remarkable for its nonmammillate cuticle and for the fringed body setae of the larvae. Little biological information is available for any of the species.

The subgenus Subparmatius consists of three bat parasites present in Central and South America. Notable features of the species are unique ventral sclerotized plates, a pointed hypostome and pulvilli on all adults and nymphs (Cooley and Kohls, 1944). Hoogstraal (1985) hypothesized that Subparmatius and the genera Antricola and Nochoaspis represent two separate branches from a common base in the subgenus Alectorobius, with the latter two genera differing more distinctively than Subparmatius from the typical Ornithodoros.

The subgenus Alveonasus consists of six species present in the Old World which feed on a wide variety of animals. This subgenus is quite distinct morphologically and its subgeneric classification represents the most notable dichotomy between the Western and Russian systematic systems with the Russians recognizing it as a genus (Pospelova-Shtrom, 1946, 1969).

The subgenus Reticulinasus is an Old World group with representation in all three geographic regions. There are nine described and three undescribed species, all of which are parasites of cave-dwelling fruit bats, usually Rousettus spp. (Hoogstraal, 1985). Only for O. (R.) salahi Hoogstraal have any biological data been published (Hoogstraal, 1953a).

There are seven species in which subgeneric affiliations have not been defined (Kohls et al., 1965). These are O. cooleyi McIvor, a parasite of western U.S. carnivores; O. elongatus Kohls, Clifford and Sonenshine, a larva from Dominican Republic with an unknown host; O. natalinus Cerny and Dusbabek, a Cuban bat parasite; O. nattereri Warburton from Brazil; O. aragasi Fonseca and O. davisii Fonseca from nests of rats (Oryzomys spp.) in Peru. The last is O. rudis Karschan imported parasite in Central and South America of rodent nests, chicken coops and humans (Dunn, 1927).

Small Genera: Otobius, Antricola and Nothaspis

The genus Otobius has only two species O. megnini (Duges) and O. lagophilus Cooley and Kohls. These species from western North America adapted to parasitize roaming mammals in the arid and semi-arid biomes (Hoogstraal, 1985). Otobius megnini parasitizes the ears of deer, Odocoileus; pronghorn antelope, Antilocapra; domestic cattle; horses; sheep; goats; dogs and occasionally man (Cooley and Kohls, 1944). Otobius lagophilus parasitizes the ears of rabbits (Silvilagus) and jackrabbits (Lepus).

The genus Antricola contains nine species in two subgenera. They are specialized parasites of insectivorous bats in the New World. Antricola (A.) coprophilus McIntosh is found in the western states bordering Mexico, A.(A.) mexicanus Hoffman in Central America and A.(Parantricola) marginatus (Banks) in Cuba and Puerto Rico (Cooley and Kohls, 1944). All other species are known only from Cuba (de la Cruz, 1976, 1978a,b).

The genus Nothaspis is represented by a single species, N. reddelli Keirans and Clifford. The species was found in guano with Antricola mexicanus parasitizing Mormoops bats in Mexico (Keirans et al., 1977b).

Life Cycles: Laboratory and Field

The life cycle of the Argasidae, as previously mentioned, consists of eggs, larvae, several nymphal stages and an adult stage that can have multiple reproductive cycles. Between each genus, subgenus or even species there are variations in the life cycle. Such variations are either manifested as variable numbers of nymphal stages or in the duration of a stages' feeding on the host: short (minutes), long (days) or none. During the course of time, coevolution of the ticks with their hosts has favored this diversity of the life cycle (Hoogstraal and Kim, 1985). So the comparison of various life cycles of ticks in relation to the hosts they parasitize shows the optimum strategies for survival and allows inferences to be drawn on the mechanisms that contribute to this optimum developmental pattern.

Argas

The life cycles of most members of Argas are characterized by slow feeding larvae (days) and fast feeding nymphs and adults (30-120 min.). There are usually two to four nymphal stages (Kettle, 1984). The development and reproductive pattern of nondiapausing Argas (A.) africolumbae Hoogstraal, Kaiser, Walker, Ledger and Converse indicate that two to three generations could

develop annually on chickens (Kraiss and Gothe, 1982). Khalil (1979) found that the life cycle of A.(P.) persicus (Oken) with low host availability could extend to more than two years, but that 18 generations per year could occur under optimal conditions.

Developmental diapause is not uncommon in Argas species. In the Moscow area, Frolov (1971) found that female A.(P.) persicus underwent diapause. Kaiser (1966a) found that female A.(P.) arboreus Kaiser, Hoogstraal and Kohls collected in the winter would hold off egg laying for several weeks. Confirmation of naturally diapausing females was found in a field study of A.(P.) arboreus in an Egyptian rookery (Guiris, 1971). This diapausing condition serves to synchronize host availability with the emergence of the larva, the tick's most susceptible stage.

The life cycles of the bat-parasitizing species of Argas show some unique developmental alterations that probably evolved in response to the rarity of feeding opportunities in the caves and shelters where they are found. The field biology of these species has not been reported.

The life cycle of the widely distributed A.(Carios) vespertilionis (Latreille) was described by Hoogstraal (1956, 1958). The females lay 3 to 4 batches of between 35 and 50 eggs over a 12 month period. The larval feeding

period on the bat is usually 17 to 19 days. There are two nymphal stages which feed for short periods. Most adults emerge from the second molt. The developmental time varies from 56 to 80 days. The emerged female commences egg laying no earlier than 13 weeks post emergence, after at least two blood meals.

The life cycle of two of the Chiropterargas species, A.(C.) boueti Roubaud and Colas-Belcour and confusus Hoogstraal was described by Hoogstraal (1956). Argas (C.) boueti females lay their eggs on vertical surfaces. The larvae feed on the bats from 8-42 days but usually 16-25 days. The first and second nymphal stages do not feed. Adults emerge after the second molt. Occasionally a third nymphal stage occurs and it will feed prior to molting to an adult. The life cycle can be completed in less than 100 days. The life cycle of A.(C.) confusus is longer: 120-300 days. The larvae feed from 5-50 days but usually 21-27 days. The first nymphal stage does not feed. The second, third and fourth nymphal stages each feed. Adults emerge from the fourth nymphal instar.

Ornithodoros

In the genus Ornithodoros a variety of developmental modes exist. In the subgenus Ornithodoros, life cycles for O.(O.) savignyi (Patton and Craig, 1913; Cunliffe, 1922)

and O.(O.) moubata (Hoogstraal, 1956) have been studied. The females, considering their relatively large size, lay few eggs per egg batch, averaging 219 (100-417) for O.(O.) savignyi. Over the 5 to 7 feeding/egg laying period in the females' life she can lay 900 in O.(O.) savignyi and 500-1200 in O.(O.) moubata. The larvae hatch from the large egg and molt to nymphs without feeding. As many as eight nymphal instars can occur but four or five is usual, with males emerging at earlier molts than females.

Life cycle studies of several Pavlovskyella species has shown that the larvae, nymphs and adults are rapid feeders. An exception is Ornithodoros (P.) tartakovski Olenov whose nymphs and adults in winter are known to remain attached to the hosts for several days (Hoogstraal, 1985). The life cycles have from two to five nymphal stages, males frequently emerging at earlier molts, usually third or fourth instar, than females, normally fourth or fifth instars. Balashov (1968) states that there is only one gonotropic cycle per year, occurring in the warm season for O.(P.) tholozani Laboulbene and Megin and O.(P.) verrucosus Olenov, Zesukhin and Fenyuk, but two in O.(P.) tartakovski under favorable conditions. Life spans can exceed 23 years (Pavlovskii and Skrynnik, 1960).

Autogeny, the production of viable eggs without a meal, as an adult is known from four species of Ornithodoros.

All four are Pavlovskyella species. Feldman-Muhsam (1973) reported autogeny in O. tholozani, O. tartakovskyi and O. parkeri Cooley with a more detailed comparison of anautogenous and autogenous females productivity in O. tholozani (Feldman-Muhsam and Havivi, 1973). Although not reported to occur in laboratory colonies of O. arenicolous Hoogstraal by Feldman-Muhsam, Hoogstraal (1953b) reports that autogeny occurs with field collected individuals.

Loomis (1961) described the life cycle of O. (Ornamentum) coriaceus from data obtained in his laboratory and from several earlier researchers. It was found that as many as seven molts occur, but that most individuals molt to adults after the fifth nymphal stage. The life cycle in the laboratory takes 15 months but probably needs no less than two years in the field. The larvae feed on the host for 7 to 10 days with the first two nymphal stages being non-feeding (Clifford et al., 1964).

The life cycle of Alectorobius is known for several species. In bats, the life cycles of O. (A.) kelleyi Cooley and Kohls and O. (A.) tadaridae Cerny and Dusbabek have been followed in the laboratory. Sonenshine and Anastos (1960) reared O. (A.) kelleyi. The life cycle consists of eggs, larvae, 2 to 4 nymphal instars and adults. They found the time span for the cycle varied from 54-258 days. The larvae fed on wild bats stayed attached longer, 9 to 20

days (15.4 mean), versus 8 to 18 days (12.2 mean) on white rats. The first nymphal stage was non-feeding. Males emerged from the second or third nymphal molts, whereas females emerged from the third or fourth nymphal molts. Nymphal and adult feeding time rarely exceeded 1.5 hours. The Cuban O.(A.) tadaridae feeds mostly on bats that roost in palm trees and its life cycle was examined by Honzakova et al. (1983). In this case, larval feeding was shorter (6-13 days) and adult feeding longer (10 hours). This species fed in the first nymphal instar. Hoogstraal (1985) states that in those O. (Alectrobius) species that feed on bats a feeding first nymphal instar is normal.

In all other Alectrobius species for which life cycle information is known, the first nymphal instar is non-feeding. This is known from the rodent feeding species: O.(A.) talaje (Guerin-Meneville) (Davis, 1942c), O.(A.) puertoricensis Fox and O.(A.) dugesi Mazzotti (Davis, 1955) and the bird parasitizing species: O.(A.) concanensis Cooley and Kohls (Davis, 1942c) and O.(A.) coniceps Canistrini (Davis and Mavras, 1956). In O.(A.) puertoricensis the span from larvae to adult varied from one month to six weeks with males emerging from the third nymphal instar and females from the fourth and fifth (Fox, 1947; Davis, 1955).

In the marine bird parasitizing Ornithodoros capensis group, life cycles have been reported for four species: O.(A.) muesebecki Hoogstraal (Hoogstraal et al., 1970), O.(A.) coniceps (Hoogstraal et al., 1979a), O.(A.) amblus Chamberlin (Khalil and Hoogstraal, 1981) and O.(A.) spheniscus Hoogstraal, Wassef, Hays and Keirans (Hoogstraal et al., 1985). In those examined, there was a long feeding period (4 to 23 days) for larvae and a non-feeding first nymphal instar. As many as six or seven nymphal instars were found, with adults emerging after the fourth. Minimum life cycle length was under six months in optimum laboratory conditions. Pavlovskii and Skrynnik (1960) reported a maximum lifespan of 4 years for O.(A.) coniceps.

The life cycle of Otobius species is different from most soft ticks. Otobius megnini larvae hatch from eggs after 11 days in summer and 3-8 weeks in cooler weather. The larvae attach in the ear and remain attached 5-11 days. The two nymphal stages can remain attached for as long as seven months, but two to three months is normal. The engorged second instar nymphs drop off and crawl up to some dry crevice or crack and molt. Adults possess non-functional mouthparts. Males live for up to 160 days (average 100 days) with females living as long as 638 days producing from 358 to 1546 eggs (averaging 814 eggs) (Hooker et al., 1912). Otobius lagophilus has a similar life cycle

with females averaging 175 eggs (100-250) (Hopla, 1955). Nymphs appear not to be restricted to the ears, having been collected while attached to the throat and jaw.

Antricola and Nothaspis

Antricola adults do not feed and have a nonfunctional short hypostome. Only the larvae have been collected on bats, but engorged nymphs have been collected (Hoogstraal, 1985; de la Cruz, 1976; Cooley and Kohls, 1944). In Nothaspis the males have a nonfunctional hypostome and the female is unknown. Nymphs are physically capable of feeding (Keirans and Clifford, 1975). Larval identity is unclear, so no conclusions can be drawn on the its feeding ability.

Ecological Niches Utilized by the Argasidae

Troglodytic Niches

The life styles of species in the family Argasidae can be grouped under three headings: Troglodytic (hole dwellers), niticolous (nest dwellers) and free living. This classification provides for easier comprehension of the host-parasite ecological interrelationships. Classification of soft ticks on this basis does not reflect taxonomic classification.

There are three subgroups of troglodytic niches: burrows, caves and xeric shelters. There are a number of varieties of burrows utilized by one or more species of soft tick: large burrows (warthogs, foxes and other canines), small burrows (burrowing owls, shearwaters, penguins and other marine birds) and reptile burrows (tortoises and lizards). Caves are used by bats, birds (falcons, swallows, sparrows, etc.), and small mammals, all of which are parasitized in these habitats by argasids. Xeric shelters are a variety of cave habitat in which the external environmental conditions, except rainfall, are relatively unmodified. Examples of this type are shallow caves, cliff overhangs, primitive livestock sheds and human dwellings. Members of the genus Ornithodoros are the predominant species that have specialized in parasitizing troglodytic niches. However cave bat specialization is found in some Argas subgenera and two Ornithodoros derived genera: Antricola and Nothaspis (Hoogstraal, 1985).

Niticolous Habitats

Most niticolous habitats are provided by birds but some by mammals also living in nests. Nest habitats include not only the familiar vegetation or mud constructed nests, but also substrate nests used by many marine birds, raptors, doves and pigeons. Mammalian nest constructors

parasitized by argasids include squirrels, rock hyrax, mice, woodrats and other rodents. Only those niticolous habitats that are utilized for several seasons or years have argasids present. Members of the genus Argas are the predominant species involved in parasitizing niticolous habitats (Hoogstraal et al., 1979b).

Free Living Hosts

There are very few argasid species that can be classified as parasites of free living or motile host species such as antelope and deer. Argasids parasitizing this type of host have had to evolve physiological or parasitic behavioral mechanisms to circumvent the sensitivity to environmental variations, both climatic and nutritional (host availability), that appear to have restricted most other argasid species to specific habitats. The only argasid species that are classified as using this type of host are Ornithodoros O. savignyi, O. O. coriaceus, O. P. gurneyi Warburton, and the two Otobius species, O. megnini and O. lagophilus.

Pathogens Associated with Argasid Ticks

Argasid ticks transmit a wide variety of infectious disease agents. With the exception of African tick-borne relapsing fever caused by Borrelia duttoni (Novy and Knapp)

vectored by O.(O.) moubata (Felsenfeld, 1971), all are zoonoses, intertransmissible between animals or man. The ability of soft ticks to serve not only as vectors, but also as reservoirs significantly affects the focality and epidemiology of the diseases. The range of disease agents vectored by Argas and Ornithodoros include RNA and DNA viruses, rickettsia, spirochetes, protozoa and nematodes. Pavlovski (1960) classified foci of vectored illnesses by their biological, abiotic and geographic features. Since argasid ticks generally are confined to very specific habitats, e.g., caves, burrows, cliff faces, bird nests, etc., and their probability of individual survival out of these habitats is low (Aviva et al., 1973), the natural focus of most Argas and Ornithodoros vectored diseases is limited to small areas of the biotype. So, in most cases, these agents present little threat to man or his livestock. Exceptions to this statement apparently are confined to those zoonoses (1) in which a polyvectoral foci exists with the second vector being more environmentally motile, such as mosquitoes and hard ticks or (2) where human activity either comes into contact with or generates an ecologically similar foci to the autochthonous foci thus allowing disease and/or vector crossover to the domestic habitat. The following is a discussion on the focality of argasid transmitted diseases based upon the commonality of niche

specialization in the various species of the family Argasidae.

Burrow Habitats

Most burrows are constructed by small animals but a few larger animals also construct them. Examples are warthogs in the family Suidae and many canids such as foxes, coyotes and jackals. In the burrows of warthogs are found Ornithodoros porcinus, the reservoir vector of African swine fever virus, and several other species in the O.(O.) moubata complex including O.(O.) moubata and O.(O.) apertus (Walton, 1979).

In Africa Ornithodoros (O.) porcinus is infected and the African swine fever virus is transmitted transtadially, sexually and transovarially (Plowright et al., 1970, 1974), with the tick serving as vector, amplifier and reservoir for the disease. In Africa, the virus circulates between the tick and the warthog and bushpig in the burrows the swine excavate (Thomson et al., 1980; Plowright et al., 1969). In these wild swine, infection does not lead to death, but in domestic swine death is common. Primary outbreaks of ASF in domestic swine was believed to be due to contact with "carrier" wild pigs but this can be discounted (Thomson, 1985). Thomson provided evidence showing that Ornithodoros species can be found in high

numbers on warthogs away from the burrow generating support for the theory of Plowright et al. (1969) that ASF infected ticks could be transported to the vicinity of domestic pigs either by warthogs or on the carcasses of warthogs. Ticks dislodged there could remain a potential source of infection for many months. This phoretic dispersal of soft ticks also explains how a giant forest hog, a solitary forest dweller, might encounter an infected tick.

The Ornithodoros moubata complex has served as a laboratory vector of several important pathogens. Ornithodoros moubata strains of unknown origin have been shown to vector Coxiella burneti (Derrick) (Q fever) (Davis, 1943c), Francisella tularensis (McCoy and Chapin) (Tularemia) (Burgdorfer and Owens, 1956) and Leptospira interrogans (Stimson) (Burgdorfer, 1956; Strickland, 1984). Similar ability to vector these diseases was shown, also by the authors, in the small burrow inhabiting, rodent-parasitizing, species: O.(P.) parkeri, O.(P.) turicata and O.(P.) hermsi Wheeler, Herms and Meyer. Rocky Mountain spotted fever (RMSF) caused by Rickettsia rickettsi (Wolbach) can be vectored experimentally by O.(P.) parkeri (Davis, 1942a,b) and O.(P.) rostratus Aragao (Davis, 1943b). Several other argasids are able to be infected by RMSF, but not able to vector it: O.(P.) turicata (Davis, 1942a,b, 1943a), O. rudis (Davis, 1943b; Hoogstraal, 1967)

and O. (P.) nicolleti and Otobius lagophilus (Hoogstraal, 1967). The European ixodid vectored pathogen Rickettsia sibirica Zdrodovskii (=R. slovaca) was found in A. (P.) persicus infecting poultry in Armenian SSR (Rehacek et al., 1977). No published field data implicate any of these ticks as significant factors in the epidemiology of these diseases. However, all of these agents are significant diseases of burrow-dwelling rodents and livestock, and the possibility that argasids may serve as secondary vectors and reservoirs of these diseases might aid in the stability of these diseases in the biocenosis.

Natural transmission of Q fever by burrow-inhabiting Ornithodoros has been demonstrated, but the epidemiological significance of this transmission is questionable (Hoogstraal, 1985). Balashov (1968) reviewed data that O. (P.) tholozani is involved in the natural transmission of Coxiella burneti (Derrick) in the warm deserts of the USSR. Ornithodoros (P.) maroccanus Velu (O. erraticus "large form") outside Casablanca, Morocco, parasitizes rabbits, Oryctolagus cuniculus (L.) that were naturally infected with C. burneti and the ticks transmitted the agent in the laboratory to guinea pigs during feeding (Blanc and Bruneau, 1955).

In North America the two small burrow-inhabiting tick species are O. (P.) turicata and O. (P.) parkeri.

Ornithodoros (P.) turicata is also found in numerous small, usually shallow caves and, occasionally, livestock pens. Cooley and Kohls (1944) report the hosts of O.(P.) turicata to be rattlesnakes, turtles, tortoises, burrowing owls, ground squirrels, prairie dogs, woodrats, rabbits, pigs, cattle, horses and man. Beck et al. (1986) recognized two subspecies of this tick, with the disjunct peninsular Florida population having the name O. t. americanus. Besides the physical separation they discuss life cycle and biological differences.

Ornithodoros (P.) parkeri is a close relative of O.(P.) turicata (Cooley and Kohls, 1944). It is a parasite in the burrows of ground squirrels, prairie dogs and burrowing owls in the western United States. Its range is more northern than O.(P.) turicata (Cooley and Kohls, 1944). Its life cycle is shorter with up to five nymphal stages, but adults begin emerging from second nymphal stages (Davis, 1941b). This shorter life cycle may be evolutionary favored in the cooler climate it inhabits because of the imposed shortened seasonal activity period.

The only diseases transmitted normally by these two Ornithodoros species are Borrelia. Borrelia classification difficulties (antigenic drift, serological variations and mutations) led to the belief in tick specificity of the respective species, which were often named after the

species of Ornithodoros from which they were isolated (Felsenfeld, 1979). However, laboratory experiments transmitting one Borrelia species to another tick that does not carry it naturally or from a louse to a tick are often successful. Hence, there was a trend toward the recognition of one Borrelia species with the tick adapted strains being recognized as variants or subspecies (Felsenfeld, 1979). For practical and epidemiological reasons the multispecies concept is adhered to in this discussion.

In the two species O.(P.) turicata and O.(P.) parkeri the Borrelia species are turicatae and parkerii. The ticks serve not only as the vectors of these diseases, but also as amplifiers and reservoirs through transtadial survival and transovarial transmission (Davis, 1941a, 1942a,b,c, 1943b). Felsenfeld (1979) proposed the hypothesis that borreliae are primarily symbionts and parasites of ticks, that have specialized in Ornithodoros species by genetic evolution and adaptation and that vertebrate invasion is an evolutionary accident. However, the fact that uninfected ticks can pick up the infection from a host with a spirochetemia (Davis, 1941a), and that highly virulent strains that produce high spirochetemia in the host are maintained in nature (Felsenfeld, 1971), suggests that the ability of Borrelia to infect vertebrates is evolutionary

avored as a mechanism of increasing the percentage of tick infections since transtadial and transovarial mechanisms are not completely effective (Gaber et al., 1984).

Borreliosis due to infection from O.(P.) turicata and O.(P.) parkeri bites or contact with coxal fluid is rare in man. Burgdorfer (1980) stated that of 280 cases of relapsing fever in the U.S. (1954-1978), only 30 cases could be attributed to B. turicatae (Brumpt) and none to B. parkerii Davis. The greater number of cases of B. turicatae is probably due to its vector being adapted for survival in a wider variety of habitats (Cooley and Kohls, 1944) that come in contact with man and his activities. Primarily these species are zoonoses of ticks and burrowing rodents (Davis, 1942a, 1943b).

In the Neotropics, three species (O.(P.) furcosus Neumann, O.(P.) braziliensis Aragao and O.(P.) rostratus) exist that are primarily parasites of burrowing rodents, but commonly attack man, dogs, livestock and peccary (Hoogstraal, 1985). Only O.(P.) braziliensis is known to carry a disease: B. braziliensis. Ornithodoros (A.) puertoricensis, a Caribbean species, parasitizes Rattus and iguanids in burrows and is a potential vector of ASF in this region (Butler et al., 1985).

In the African region there are twelve species that are parasites of burrowing animals, eight of them are not

present elsewhere. All of these eight species are known from several geographic areas and are presently epidemiologically insignificant. These eight are represented by Ornithodoros (O.) compactus which parasitizes tortoises, Testudo spp. in scrapes south of the Zambezi River (Walton, 1962); O.(A.) delanoei Roubaud and Colas-Belcour from burrows and caves and parasitizing hedgehogs, porcupines and small rodents across North Africa (Hoogstraal, 1956, 1985); O.(A.) eboris Theiler from a few specimens collected in a porcupine burrow in South Africa (Hoogstraal, 1985); O.(P.) normandi Larrousse a parasite in rodent burrows in Tunisia (Hoogstraal, 1956); O.(P.) sonrai a parasite of the grass rat (Arvicanthis) in Senegal (Wallis and Miller, 1983); O.(P.) zumpti inhabits burrows of the striped mouse, Rhabdomys pumilio (Sparrman) and other rodents in Cape Province, South Africa (Hoogstraal, 1956); O.(P.) arenicolous in North African mammal burrows (Hoogstraal, 1953b) and O.(P.) greinieri from lowland forest burrows of the endangered rodent Hypogeomys antimena Grandidier in Madagascar (Hoogstraal, 1985).

There is little disease transmission in these African endemics. From these species in the Ornithodoros and Alveonasus subgenera no diseases have been reported. In the Pavlovskyella species both viruses and borreliæ are known. Borrelia tillae Zumpt and Organ is known from

O.(P.) zumpti (Zumpt and Organ, 1961) and a Borrelia strain was found in O.(P.) normandi (Hoogstraal, 1956). Because of confusion in the literature in separating O.(P.) sonrai from O.(P.) erraticus, the reports of a Borrelia in O.(P.) sonrai need to be re-examined. Wallis and Miller (1983) point out that the two species are separable, not only biochemically, but by the respective Nairovirus they each vector; Qalyub virus in O.(P.) erraticus and Bandia in O.(P.) sonrai. These two members of the Qalyub serogroup (Bunyaviridae) are not only vectored by ticks, but the ticks are also the reservoirs for these viruses (Hoogstraal, 1985).

The Palearctic region shares with Africa several rodent burrow parasitizing argasids. Some are the most prominent in epidemiological importance in the whole family. They are O.(P.) erraticus, O.(P.) tholozani, O.(P.) morocanus and O.(A.) foleyi Parrot. Ornithodoros (A.) foleyi is the exception, since this desert species has had no virus or spirochetes isolated from it (Hoogstraal, 1985). Although O.(P.) tholozani is known from burrows, its importance as a vector is related to its activities in caves and animal shelters and will be discussed in the next section.

The most recently prominent member of this group is O.(P.) morocanus, a species previously synonymous with O.(P.) erraticus that is found in Spain, Portugal and

northwestern Africa (Hoogstraal, 1985). This tick is the vector and reservoir of E. hispanica (de Buen), the causative agent of Hispano-African tick-borne relapsing fever (Felsenfeld, 1979). Following the introduction of ASF virus into Portugal and Spain (between 1957 and 1960) this tick became infected with the virus and the disease became endemic (Wilkinson, 1981). Like O.(P.) tholozani, but not like O.(P.) erraticus, this tick species infests not only burrows, but also stables and pens of domestic livestock, especially in cooler or mountain regions (Pospelova-Strom, 1953; Hoogstraal, 1985). Avivi et al. (1973) correlated O.(P.) tholozani migration out of the protected cave and burrow habitat with atmospheric relative humidity.

Ornithodoros (P.) erraticus is distributed from northern Africa, across northern Arabia, to Turkey, southwestern USSR and into Iran. Hoogstraal (1985) considers O.(P.) alactagalis and O.(P.) neerensis to be junior synonyms. Hoogstraal et al. (1954) studied this species in Egypt discovering in the rodent burrows it parasitizes a wide variety of rodents, lizards, burrowing owls and even a toad (Bufo spp.). There may be two generations annually.

A wide variety of diseases are transmitted by this species. Qalyub virus (Nairovirus) in Egypt (Wallis and

Miller, 1983) and Artashat virus (Bunyaviridae, unclassified serogroup) in Armenian SSR (L'vov et al., 1975b) were isolated from this species. Qalyub virus replication and transmission in the tick was examined by Miller et al. (1985). The only piroplasm vectored by a soft tick, Babesia (Nuttallia) meri Gunders is transmitted by O.(P.) erraticus (Gunders and Hadani, 1974). The piroplasm infects the fat sand rat, Psammomys obesus Cretzschmar. Several hard ticks and O.(P.) tholozani that parasitize the rat, were incapable of transmitting the agent.

Borrelia crocidurae (Leger), the causative agent of North African relapsing fever, is vectored by O.(P.) erraticus. Gaber et al. (1984) provided distribution, host information, ecology, seasonal dynamics and transmission information. The other local Ornithodoros tick in Egypt, O.(O.) savignyi that has never been found to be infected in nature, was also examined for spirochete transmission. The sand tampan O.(O.) savignyi could harbor it transtadially but not transovarially.

Hyperparasitism is very common in O.(P.) erraticus and this could serve to increase the overall incidence rate of infection in the tick population (Helmy et al., 1983). The report also summarizes evidence on six other argasid species, including O.(P.) tholozani and O.(P.)

tartakovskiyi, that have been observed to hyperparasitize, and all are associated with Borrelia transmission.

Human lice, Pediculus humanus, biting B. crocidurae-infected animals easily acquire and maintain the infection (Haberhorn, 1963a,b). Thus, louse-infested persons who are bitten by infected O.(P.) erraticus may experience tick-borne relapsing fever and serve as a source of louse-borne B. crocidurae (Gaber et al., 1984). Hoogstraal (1985) expressed the hypothesis that the epidemic of louse-borne relapsing fever in Egypt and North Africa after World War II may have been due to this spirochete, and not to Borrelia recurrentis (Lebert).

In the Palearctic region, excluding North Africa, the remaining burrow inhabiting species are O.(P.) tartakovskiyi, O.(P.) cholodkovski Pavlovsky and O.(P.) asperus Warburton. Ornithodoros (P.) tartakovskiyi, the most significant epidemiologically, is distributed in southern Russia, Iran, Afghanistan and China (Fillippova, 1966). It inhabits the burrows of rodents and small carnivores, as well as the resting places of hedgehogs, tortoises, other reptiles and, infrequently, shelters of livestock. Its life cycle may be completed in three to four months or may extend to two years. Unlike other Pavlovskyella species, it is known for remaining attached to the host for long periods of time especially in the

winter (Hoogstraal, 1985). It can survive 12 years under laboratory conditions (Pavlovskii and Skrynnik, 1960).

Ornithodoros (P.) tartakovskyi is the natural vector of the filarial worm Dipetalonema viteae Krepkogorskaja that infects central Asian gerbils (Hoogstraal, 1985). Borrelia latyschevii (Sofiev), the causative agent of Central Asian relapsing fever, is transmitted by O.(P.) tartakovskyi and causes a mild disease. Another severe disease causing agent is Borrelia caucasica Kandelaki transmitted by O.(P.) asperus (O.(P.) verracosus ?) (Felsenfeld, 1971). Plague has been associated with O.(P.) tartakovskyi (Hoogstraal, 1985).

Chim virus is found in both argasids, (O.(P.) tartakovskyi and O.(P.) tholozani) and ixodids (Rhipicephalus (R.) turanicus) Pomerantsev, that inhabit the burrows of the great gerbil in Uzbek SSR (L'vov et al., 1979).

Caves and Shelters

This category is an ecological catch-all in that its premise, a natural geological shelter, or an artificial shelter that architecturally simulates a natural one, with xeric conditions but with ambient or high relative humidity, is ecologically quite wide. The subcategories, sheds and houses, overhangs and shallow caves, and deep

caves were defined on ecological and epidemiological parameters.

Sheds and Houses

Several species have adapted to become synanthropic. The two most important are Ornithodoros (O.) moubata "domestic race" and O.(O.) porcinus domesticus. These are associated not only with some homes in most of Africa, but also with domestic animal enclosures and pigsties, where ASFV might circulate (Haresnape and Mamu, 1986).

African relapsing fever, Borrelia duttoni, circulates only between these ticks and man in domestic situations. The disease is distributed through most of sub-Saharan, East and South Africa. The development of an infection in the tick is typical of all known Ornithodoros spirochete infections (Geigy, 1968). The Borrelia are passed both transtadially and transovarially. The highest spirochete densities develop in young nymphs and adults in the salivary glands, but in older females in the ovaries. Transmission of the agent to the mammalian host is usually by bite, but coxal gland fluid is often infective if it can reach an open wound.

In central and northern South America, Ornithodoros rudis apparently has developed a similar relationship where it parasitizes both man and livestock (Cooley and Kohls,

1944) in addition to its normal rodent hosts. This tick transmits Borrelia venezuelensis Brumpt (=neotropicalis) (Felsenfeld, 1971, 1979). Transovarial transmission of the spirochete has not been observed in this tick (Felsenfeld, 1979). There are only two soft tick species outside the subgenus Pavlovskyella that transmit a mammalian infecting Borrelia zoonoses, O. rudis is one and the other is, O.(O.) coriaceus (Hoogstraal, 1985). Ornithodoros rudis has also been associated with domestic situations in which Rocky Mountain spotted fever (RMSF) circulated (Hoogstraal, 1967).

The remainder of the species that infect houses and sheds are primarily livestock pests. These include O.(P.) tholozani, O.(P.) morocanus (previously discussed), O.(P.) turicata (previously discussed), O.(A.) canestrinii (Birula) and O.(A.) lahorensis Neumann. These are all species that have undergone niche crossover, the Pavlovskyella species from burrows and the Alveonasus species from shallow caves and overhangs.

Ornithodoros (P.) tholozani is a widely distributed Old World species found from Libya through the Near East and Greece through southern Russia, northern India into southwestern China. It is referred to as O.(P.) papillipes and O.(P.) crossi in the Soviet and Indian literature respectively. Aviva et al. (1973) studied the ecological

parameters of its survival in caves in Israel. Pospelova-Shtrom (1953) found that in Russia it was present only in those caves, houses or animal shelters with temperatures of 24-25°C and a relative humidity of 70-75%. In Turkmenistan, the tick can be found in cool mountain elevations in more exposed natural shelters, such as under rocks, but in the dry foothills only in caves and burrows. In Israeli caves that house animals continuously, tick populations can be high. In those caves that are used infrequently, tick population numbers differ greatly, but usually numbers decrease with only late nymphs and females present. These ticks are deeply buried in the soil and do not emerge to attack casual cave inhabitants (Avivi et al., 1973).

The known hosts are reviewed by Hoogstraal (1985). They include man, sheep, goats, porcupines (Hystrix), hedgehogs (Hemiechinus, Paraechinus), foxes, badgers, jackals (Canis) and numerous rodents. Camels, cattle and birds, including chickens, also serve as hosts.

Ornithodoros (P.) tholozani is known to be involved in two Flavivirus species zoonoses. West Nile virus was isolated from the tick (L'vov et al., 1975a). This virus normally circulates between culicine mosquitoes and birds, occasionally affecting man (Berge, 1975). Karshi virus was found in O.(O.) tholozani and Hyalomma asiaticum, two

parasites of the great gerbil, Rhombomys opimus (Lichtenstein), in Russia (L'vov et al., 1976; Hoogstraal, 1985). Chim virus, previously mentioned, also circulates between argasids and ixodids in the burrows of this gerbil (L'vov et al., 1979).

Associated with O.(P.) tholozani is the pernicious Persian relapsing fever, Borrelia persica (Dschunkowsky) (Felsenfeld, 1971, 1979). This tick's adaptability and ready acceptance of man, his domestic animals and domestic rodents as sources for blood meals (Balashov, 1968; Hoogstraal, 1981) provides opportunity for human infections. Additionally, lice are known to pick up B. persica (Felsenfeld, 1971) thus increasing the epidemiological importance of this tick.

The most important species in the subgenus Alveonasus is O.(A.) lahorensis. It was originally a parasite of the Asiatic mouflon, Ovis aries Linnaeus and other wandering ungulates that rested on cliff faces, but is now a notorious parasite of domestic sheep, goats, camels and cattle in western China, Pakistan and from southern Russia to Saudi Arabia (Fillippova, 1966). In Russia this tick has become a serious parasite especially in primitive stables.

Its life cycle is unusual in that it resembles a two-host tick. The larvae, which can survive for a year unfed,

attach to the host for 3 to 6 weeks and drop off as third instar nymphs. After molting, the tick becomes an adult and will feed for 2-3 hours. Females can produce two egg hatches (300-500 eggs). Unfed adults can survive for 18 years (Fillippova, 1966). This life cycle and the longevity of the stages has allowed the parasite to readily adapt to parasitizing domestic animals. The developmental adaptability and high survivability of this tick places it also in the free living category. However, because of its dependence upon some form of shelter, it is included here. The unique life cycle of this tick, with long host attachment periods, is epidemiologically relevant because of the increased probability of a disease-infected tick being introduced to an area where it may serve as the source of a new disease foci. Its long lifespan means a reservoir exists with a lifespan equal to or greater than its hosts, so it may encounter and infect one to three naive host generations during the course of its life.

Two disease agents are involved with this species. Crimean-Congo hemorrhagic fever virus was isolated from a larva collected from a horse (Sureau et al., 1980). Hoogstraal (1985) suspected the isolate came from active virus in the undigested blood meal rather than a true infection. There is a single report of Anaplasma transmission by argasids. Immature O. (A.) lahorensis

became infected with Anaplasma ovis Lestoguard when feeding on sheep and could transmit it to other sheep (Bityukov, 1953). There is also an early report by Kamil and Bilal (1938) that the tick was capable of transmitting tularemia. Kusov et al. (1962) stated that all stages are capable of transmitting Q fever and the association between this tick and domestic animals implicates it in the epidemiology of the disease.

Ornithodoros (A.) canestrinii is found in Iran and Turkmen SSR. It parasitizes wild sheep, goats and gazelles in caves or overhangs. Domestic animals are also parasitized in stables (Hoogstraal, 1985). Kusov (1973) reported its biology. He reported the life cycle may require 10-16 years. Presently no diseases are known to be vectored by this species.

Shallow Caves and Overhangs

A variety of species in several subgenera of Ornithodoros and Argas have adapted to parasitizing hosts in shallow caves and overhangs. Two O. (Alveonasus) species: foleyi and acinus Whittick parasitize large animals sheltering in these habitats (Hoogstraal, 1985). Numerous O. (Pavlovskyella) species utilize this habitat in addition to burrows but O.(P.) graingeri Heish and Guggisberg, the spirochete host for B. graingeri Heish

(Heisch, 1953), is specifically known from cave habitats (Hoogstraal, 1956; Condry et al., 1980). The three Argas (Secretargas) species live in this habitat type but, unlike the bat-parasitizing African species, the species from Madagascar utilize a "micro" version provided by small to medium size rocks (Hoogstraal et al., 1984). The most unusual among all of these is A.(A.) cucumerinus. This species has developed a quick feeding larva (all other subgenus Argas species use a longer feeding period) and parasitizes marine birds that rest but do not nest on the Peruvian sea cliffs where these ticks reside (Clifford et al., 1978).

Deep Caves

All cavernicolous species included in this section are parasites of bats, except for the Australian falcon parasite, A.(A.) lowryae Kaiser and Hoogstraal, in which the single collection came from birds which were nesting in a cave (Kaiser and Hoogstraal, 1975). In the Old World, insectivorous bats are parasitized by species in the subgenera A. (Carios) and A. (Chiropterargas) (Hoogstraal, 1956, 1985) and cave dwelling fruit bats by the subgenus O. (Reticulinasus) (Hoogstraal, 1953). In the New World only Ornithodorinae species parasitize bats. Bats are the sole hosts of the subgenus Subpamatus, and the genera Antricola

and Nothaspis. About half of the species in the O. (Allectorobius) subgenus have bats as their sole known host.

Kyasanur Forest disease (KFD) virus was isolated from O.(R.) chiopterphila Dhanda and Rajagopalan, a fruit bat parasite in India (Dhanda and Rajagopalan, 1971). Normally KFD is a disease transmitted by hard ticks, especially Haemaphysalis, in which transtadial but not transovarial transmission occurs (Hoogstraal, 1966, 1981). Experimentally, transtadial, transovarial and F₁ transmission of KFD to susceptible hosts have been demonstrated for A.(P.) persicus (Sengh et al., 1971) and O.(P.) tholozani (Bhat and Goverdhan, 1973). The importance of any of these ticks in the transmission cycle of this disease is unclear (Hoogstraal, 1985). Two serologically ungrouped viruses were isolated from O. Reticulinasus species: one from Muroor, India, in the tick O.(R.) piriformis Warburton (Sreeivasan et al., 1983) and one from an undescribed species in Chobar Gorge, Nepal (Berge, 1975).

Another bat associated Flavivirus species is Sokuluk, isolated from the insectivorous bat-feeding A.(C.) vespertilionis in southern Russia (L'vov et al., 1973). Hoogstraal (1980) suspects that Keterah virus from A.(C.) pusillus Kohls and Issyk virus from A.(C.) vespertilionis

and Ixodes (E.) vespertilionis Koch may be geographic names for the same virus. Hoogstraal (1985) reviewed data from several Russian authorities which indicate that this virus or virus complex, regarded as being associated chiefly with bats and bat-parasitizing Argas (Carios) and Ixodes ticks, should be appreciated as being more serious epidemiologically in light of demonstrated circulation between birds, mosquitoes and man.

In the New World, Estero Real virus was isolated from O.(A.) tadaridae, a bat parasite in Cuba where its circulation probably does not affect birds, humans or domestic animals (Malkova et al., 1985). Matucare virus from Bolivia was isolated from the bat parasite O.(A.) boliviensis Kohls and Clifford (Justines and Kuns, 1970). Both of these viruses were collected from atypical subgenus representatives. Both ticks feed on bats that do not utilize caves, but instead live in palm trees or, in the case of the O.(A.) boliviensis specimens mentioned, live in the palm leaf thatch of huts. Considering the ease in collecting specimens in palm trees versus caves, it is not surprising that Neotropical bat-circulating viruses were first isolated from these tick species.

Nests

Nests are defined as those habitats that have animals which either periodically utilize the site to rear young or use the nest for longer periods as a domicile, but in both cases the site must be at the substrate surface or arboreal. Some mammal domiciles meet this criteria, but birds dominate this habitat type. There are four subcategories: marine nests, ground or cliff nests, arboreal nests and rodent nests.

Marine nests

Soft ticks that parasitize marine ground nesting birds are usually in the Ornithodoros (A.) capensis group but one Argas, A.(A.) macrostigmatus also parasitizes birds in this habitat (Fillippova, 1966). Only the O.(A.) capensis group species are virus infected (Hoogstraal, 1973b). However on an inland saline lake in California where California gulls, Larus californicus Lawrence, nest is an undescribed species of tick near Argas (A.) cooleyi Kohls and Hoogstraal from which Mono Lake virus was isolated (Berge, 1975; Hoogstraal, 1985). Ornithodoros (A.) capensis, the postulated progenitor of the group has a worldwide distribution and parasitizes a variety of marine nesting birds: gulls (Larus), cormorants (Phalacrocorax), penguins, terns (Sterna), etc. (Kohls et al., 1965). It is known to

vector several viruses. Soldado virus in the "Hughes" serogroup is a complex of strains found worldwide, infecting three "capensis group" species: O.(A.) capensis, O.(A.) maritimus Hoogstraal and O.(A.) denmarki Kohls, Sonenshine and Clifford, Amblyomma loculosum Neumann and numerous birds: terns, gulls and cormorants (Chastel et al., 1983). Hughes virus, is restricted to the Caribbean and was isolated in Trinidad from O.(A.) capensis and in Florida from O.(A.) denmarki (Hughes et al., 1964) and several other Caribbean locations. The Hughes group is considered important to human health because of the risk of contact between human and infected sea birds, especially in the Mediterranean where Soldado virus caused a serious resistant rhinitis in an ornithologist (Chastel et al., 1981).

In the Pacific and off the Australian coast several viruses have been isolated in O.(A.) capensis. Midway virus infects O.(A.) capensis and O.(A.) denmarki in the Pacific where antibodies are prevalent among black tailed gulls, Larus crassirostris Vieillot (Takahashi et al., 1982). Saumarez Reef virus was isolated from O.(A.) capensis and Ixodes eudyptis Maskell parasitizing sooty terns in Australia (St. George et al., 1977). In the Quarantfil serogroup, Johnson Atoll virus is present from Hawaii, Australia, New Zealand to the coast of Namibia

(Hoogstraal, 1985). The virus has been found in O. (A.) capensis and O. (A.) denmarki and is known to affect terns, gannets and cormorants (Austin, 1978; Hoogstraal, 1985). In the Upolu serogroup, Upolu and Aransas Bay virus were isolated from O. (A.) capensis upon the Great Barrier Reef in Australia and the coast of Texas, respectively (Yunker et al., 1979).

Besides Hughes virus, three other related viruses are present in the New World (Clifford, 1979). Raza and Farallon infect O. (A.) denmarki and O. (A.) sp. near denmarki, respectively, in islands off California and Mexico. Punta Salinas virus may cause human disease in guano workers parasitized by O. (A.) amblus in Peru (Clifford et al., 1980). Huacho (HUA) virus (Orbivirus) also infects Ornithodoros (A.) amblus in Peru (Hoogstraal, 1985). In the Palearctic only two O. (A.) capensis group species are found, O. (A.) maritimus and O. (A.) muesebecki. Russian researchers have isolated West Nile virus in several bird parasitizing argasids including O. (A.) maritimus (Mirzueva et al., 1974). These ticks are probably not involved in primary transmission. Another Flavivirus species, Meaban virus was collected from O. (A.) maritimus parasitizing gulls on offshore islands in France (Chastel et al., 1985). Baku, an Orbivirus and Caspiy, a Bunyavirus, from the USSR, were isolated from O. (A.)

coniceps and O.(A.) maritimus, parasitizing pigeon nests and herring gulls, respectively (Berge, 1975; L'vov et al., 1980).

Puffin Island virus was found in O.(A.) maritimus on an island off the coast of Wales (Gould et al., 1983). Zirga virus in O.(A.) muesebecki, a parasite of boobies, cormorants, osprey and other marine birds in the Arabian Gulf may be the causative agent of blisters, pruritus and fever in people bitten by the tick (Hoogstraal and Gallagher, 1982).

In reviewing the transmission of these viruses, several similarities become evident. First the hosts of these viruses and ticks are pelagic or range over wide areas of seacoast so that the reported wide distribution of these viruses and their vector ticks is easily explained. The long feeding larvae may be transported long distances (Hoogstraal, 1973a) thus serving as the ticks migration mechanism.

Duffy (1983) studied the effects on seabirds of O.(A.) amblus and reviewed similar data of other researchers. He stated that high tick population levels are reached after four to ten years of continuous use of the site. Birds deserting the area, perhaps with attached larvae, are more likely to have encountered a virus infected tick and so the

rate of virus dissemination to other colonies is increased (Hoogstraal, 1973b, 1985).

Spread of these viruses out of the marine bird and tick colony niches is shown by Russian viral isolates found in O.(A.) coniceps, a pigeon nest parasite. This spread into the wider biocenosis of the virus can be explained perhaps by the tendency of some seabird species to nest on cliffs. Such coexistence can afford the ticks of each host the opportunity to feed on the others' host. Infected pigeons could then infect urban populations of pigeons and, subsequently, their soft tick parasites which are known to feed on man (Hoogstraal et al., 1979a; Siuda et al., 1979; Hoogstraal, 1985).

Ground or cliff nests

Pigeons, swallows, martins, raptors and house sparrows are the predominant hosts that utilize these cliff habitats. Soft ticks that parasitize birds in these habitats are predominantly in the subgenera: Argas (Argas) and Ornithodoros (Proknekalia) but the species O.(A.) coniceps, O.(A.) colloclaliae Hoogstraal, Kadarsan, Kaiser and Van Peenen and O.(A.) concanensis are also included. Ticks in these habitats are found in cracks in the walls, under debris or nests, or inside the mud nests of swallows.

Pigeons (Colomba livia Gmelin), a domesticated species, are parasitized in both wild and domestic situations with several Argas species but A.(A.) reflexus (Fabricius) (Hoogstraal and Kohls, 1960a) and A.(A.) hermanni Audouin (Hoogstraal and Kohls, 1960b) are the most predominant.

In domestic pigeon houses two Uukuvirus species were isolated (Berge, 1975). Isolates of these two have come only from these domestic sources. Grand Arbaud (GA) virus infects pigeons and their parasites, Argas (A.) reflexus, in Camarque, France. Ponteves virus was also isolated from Argas (A.) reflexus near the same location in France. Grand Arbaud virus, has also been identified in A.(A.) hermanni in Egypt (Hoogstraal, 1985).

There are a number of viruses that have been isolated from tick parasites in this subcategory that are not restricted to this habitat. These include the Flavivirus, Royal Farm and West Nile isolated from A.(A.) hermanni and O.(A.) coniceps (WN only) which also affects various mammals including man and may be vectored by ixodids (Hoogstraal, 1985; Darwish et al., 1983; Sidorova et al., 1975; Schmidt and Said, 1964).

Baku virus and Caspiy virus isolates in O.(A.) coniceps were discussed in the marine nest section. Quarantfil virus was isolated in A.(A.) hermanni and A.(A.)

vulgaris Filippova and this virus will be discussed in the section on heron rookery argasids.

In humans and other animals most argasid bites cause local irritation, minor tissue damage and sometimes pruritus (Lavoipierre and Rick, 1955). However a case was reported of induced anaphylactic shock due to the allergic response of a 59 year old Italian to the salivary toxins of A.(A.) reflexus (Miadonna et al., 1982). The ticks parasitized the pigeons that lived in the roof of her house.

Several viruses or virus groups are known that seem to be associated with either the habitat or the host type. Chenuda virus infects Argas (A.) hermanni from Egyptian pigeon houses and Ornithodoros (P.) peringueyi Bedford and Hewitt from nests of the cliff swallow Petrochelidon spilodera (Sundevall) in South Africa (Berge, 1975). Serological evidence of Chenuda virus infection has been shown for several mammals and the virus has been isolated in Culex mosquitoes that probably fed on infected migrating turtle doves (Hoogstraal, 1985). The role of these vectors in the cyclic transmission is not understood. The Abu Hammad subgroup (Nairovirus) consists of three viruses; Abu Hammad (A.(A.) hermanni), Abu Mina (A.(P.) streptopelia Hoogstraal, Kaiser and Kohls) and Pretoria (A.(A.) africanumbae), all infecting doves and pigeons and their

argasid parasites from the Ethiopian region to Iran (Darwish and Hoogstraal, 1981; Hoogstraal et al., 1975). The host and tick vectors of Abu Mina virus are found in arboreal nest habitats. The presence of seropositive mammals to Abu Hammad and Abu Mina virus indicates a wider range of virus reservoirs and vectors than is presently known (Hoogstraal, 1985).

In the western United States there are two swallow parasites: Argas (A.) cooleyi and O.(A.) concanensis. Ornithodoros (A.) concanensis has a wider host range including other birds, bats, mice and woodrats (Hopla and Loya, 1983; Cook, 1972).

Rickettsia bellii is an agent found in Ixodidae (Haemaphysalis and Dermacentor) and also in argasid bird parasites, A.(A.) cooleyi and O.(A.) concanensis described by Philip et al.(1983). There is no evidence that this agent causes human illness.

All three viruses from this habitat were isolated from Argas (A.) cooleyi: Sapphire II (Texas, Montana, New Mexico and South Dakota) (Hoogstraal, 1973b, 1985), Sunday Canyon (Texas) (Yunker et al., 1977) and Sixgun City (Texas, Colorado, New Mexico and South Dakota) (Yunker et al., 1972; Hoogstraal, 1985).

Arboreal nests

Arboreal nests are primarily the habitat of Argas (Persicargas) species. Exceptions in the New World are Argas (A.) dulus (Keirans et al., 1971), A.(A.) monachus (Keirans et al., 1973), A.(A.) brevipes (Kohls et al., 1961) and Ornithodoros (P.) macmillami Hoogstraal and Kohls in Australia (Hoogstraal and Kohls, 1966a). None of these exceptions is known to be involved in disease transmission. Epidemiologically significant tick-infested arboreal nest habitats can be divided into heron rookeries and vulture nests. Domestic poultry houses and rearing situations are also included in this category since most of the soft tick parasites involved are A. Persicargas species.

In heron rookeries, the main species involved are A.(P.) arboreus in Africa (Hoogstraal, 1985) and A.(P.) robertsi Hoogstraal, Kaiser and Kohls in the Oriental and Australian regions (Hoogstraal et al., 1975). In Florida, A.(P.) radiatus Railliet was collected from mangrove trees frequented by herons (Kohls et al., 1970).

Quarantfil virus is widely distributed in Africa and the Middle East and is reviewed by Hoogstraal (1985). This disease causes human infections but is largely a disease infecting Argas ticks and the birds they parasitize. The viral epidemiology in the tick A.(P.) arboreus has been examined together with tick species specificity for virus

infectiveness (Kaiser, 1966b,c). The fact that most mammals in affected areas carry positive antibody titers (Darwish and Hoogstraal, 1981) implicates ixodid involvement in the cycle. However, the exact interactions are unclear.

Nyamanini (NYM) virus was isolated from a cattle egret and it also infects the heron parasites; A.(P.) arboreus, A.(A.) hermanni and A.(A.) robertsi and is distributed across both Africa and the southern Palearctic region to Thailand (Hoogstraal et al., 1975; Darwish and Hoogstraal, 1981). Nyamanini virus seasonal dynamics in A.(P.) arboreus is known, with high infection rates in winter, spring and summer, and lower rates in the fall (Kaiser, 1966b). The virus is known by antibody response to also infect mammals (Berge, 1975).

The Kas Shuan (Nauovirus "Dera Ghazi Khan serogroup") subgroup consists of Kao Shuan (KS) and Pathum Thani (PT) infecting A.(P.) robertsi in Southeast Asia, Taiwan and Australia (Khalil et al., 1980). The widely distributed locations of virus illustrate how little is known about the role of bird migration in virus dispersal as the infected herons migrate back and forth between these areas. Recently, Lake Clarendon virus (unclassified and serologically ungrouped) was found in the cattle egret

parasite A.(P.) robertsi in Australia. Its maintenance in the tick is not transovarial (St. George et al., 1984).

In West Pakistan, two viruses were isolated from the vulture parasite Argas (P.) abussalami Hoogstraal and McCarty: Manawa (Urkuvirus) and Bakau (Bunyaviridae ?) (Berge, 1975; Hoogstraal, 1985). Manawa is from West Pakistan where it was isolated from Argas abussalami a vulture nest inhabitant. Subsequently, Manawa virus was isolated from two Rhipicephalus species and high antibody titers were detected in cattle, goats, humans, sheep, quail, pigeons and sparrows, indicating a need to reevaluate the natural history and importance of this agent (Darwish et al., 1983; Hoogstraal, 1985). Bakau virus also has a wide host range with isolates from Culex mosquitoes and seropositive reactions in rodents and man (Darwish et al., 1983). Argasid parasites of vultures exist worldwide but no other viral isolates have been reported.

Many Argas (Persicargas) species were collected from parasitized domestic chickens and other poultry. These tick species can become significant problems. Although virus transmission is not an apparent problem, these ticks do vector diseases and can cause avian paralysis.

Aegyptianella pullorum Carpano is the monotypic member of this piroplasm genus. It is the agent of aegyptianosis, a non-contagious disease of birds, including domestic

chickens, ducks, geese and quail. The disease and its epidemiology was reviewed by Gothe and Kreier (1977). The disease appears to be restricted to a bird-Argas cycle in temperate and tropical areas. Aegyptianella is found to develop in the gut and salivary gland of all mobile tick life stages, but transovarial transmission is rare. Overlapping generations of Argas appear to be necessary for the maintenance of the disease. Maintenance is also aided by the fact that infected chicks are infective 18 months later. The following are known to be involved in field transmission to chickens and other fowl: A.(P.) persicus, A.(P.) walkerae Kaiser and Hoogstraal, A.(P.) africolumbae, and the American A.(P.) radiatus and A.(P.) sanchezi Duges.

In Argas species, Borrelia anserina (Sakharoff), the causative agent of avian borreliosis, is found. The disease is pathenogenic to all domestic fowl. The Old World vectors are A.(P.) arboreus and A.(P.) persicus. The spread of the latter worldwide has also spread this disease (Hoogstraal et al., 1979b). In the Western Hemisphere, the Persicargas subgenus members A.(P.) sanchezi and A.(P.) miniatus Koch are implicated in transmission (Da Massa and Adler, 1979; Santos, 1982).

Using four species of Argas present in Egypt; A.(P.) persicus, A.(P.) arboreus, A.(P.) streptopelia and A.(A.) hermanni, two experimental studies were undertaken to

examine spirochete localization (Diab and Soliman, 1977) and transtadial and transovarial transmission (Zaher et al., 1977). These are model studies in Borrelia/tick transmission and specificity. They outline the variable suitability of closely allied Ornithodoros species for this Borrelia pathogen.

Avian paralysis induced by Argas infestation is not uncommon and Gothe has reviewed the subject (Gothé, 1984; Gothe et al., 1979). Avian paralysis is known to be caused by A.(A.) reflexus, A.(A.) africanus, A.(P.) persicus, A.(P.) walkerae, A.(P.) arboreus, A.(P.) radiatus, A.(P.) miniatus and A.(P.) sanchezi. Pharmacological response of the Argas toxins in relation to this problem was examined in Gothe et al. (1979). The higher the parasite load, the greater the extent and intensity of the paralysis. Older, healthy and heavier birds are less likely to succumb (Rosenstein, 1976) but no immunity is produced (Gothé, 1984).

Host immunity to argasid ticks is at best partial. Trager (1940) showed that chickens repeatedly fed upon by Argas persicus nymphs and adults developed no protective immunity. However, when the chickens were exposed to the longer feeding process of the larvae, they developed a partial immunity. In feeding A.(P.) arboreus larvae on wild (presumably pre-exposed) cattle egrets, the

engorgement period was longer when compared to naive birds (Hafez et al., 1971). Additionally, the age dependent immunity (susceptable naive chick versus older egrets) of the host is important in the transmission of Quaranfil virus by affecting the ability of the previously tick infested bird to minimize or prevent the agent to cause disease upon reexposure (Kaiser, 1966c; Hoogstraal, 1985).

Argasid ticks in mammal nests constructed above ground are primarily restricted to the Neartic. Some have become health hazards to man because of this host association. In Mexico, O. (P.) nicollei Mooser normally parasitizes woodrats, Neotoma, and ground squirrels, Citellus, but it also infests caves and rural homes (Hoffman, 1962; Kohls et al., 1965). Ornithodoros sparnus Kohls and Clifford in the western United States parasitizes Peromyscus and Neotoma (Kohls and Clifford, 1963). The biology of these two species is virtually unknown.

Ornithodoros (P.) hermsi is another western United States species, but it is found normally at high altitudes. It parasitizes small rodents such as chipmunks (Eutamias), woodrats (Neotoma) and pine squirrels (Tamiasciurus) that nest in hollow logs, stumps or cabins (Davis, 1939; Cooley and Kohls, 1944). Ornithodoros (A.) talaje (= O. dugesi ?) parasitizes a wide variety of mammals, birds and man, and

is found in houses, woodrat nests, and burrows (Cooley and Kohls, 1944; Kohls et al., 1965).

Ornithodoros (P.) hermsi, not being a burrow parasite but a nest parasite of small mammals, has ample opportunity to encounter man because it parasitizes rodents that den in cabins and "lean-to's" (Cooley and Kohls, 1944; Harwood and James, 1979). Burgdorfer (1980) demonstrated how human activity near infected nidi provides an opportunity for transmission. The statistics showed that of 280 cases of relapsing fever (1954-1978), 250 were attributed to B. hermsi Davis and 30 were B. turicatae. In Mexico and Guatemala O. (A.) talaje transmits a Borrelia, known by the name Borrelia mazzottii Davis, to man. However, distinctiveness of the strain is questionable (Felsenfeld, 1971).

Free Living Hosts

Only five species can be considered free living: Ornithodoros (O.) savignyi, O. (O.) coriaceus, O. (P.) gurneyi, Otobius lagenophilus and O. megnini. These species although restricted to dry, desert-like habitats, have evolved behavioral and physiological mechanisms that make them independent of the need for physical shelters. Three additional species could also be included but, because of their frequent collection in sheltered

situations, they are not. They are Argas (A.) cucumerinus, A.(O.) brumpti and Ornithodoros (A.) lahorensis.

The sand tampan, O.(O.) savignyi, possesses eyes, a trait shared only with one other Ornithodoros species: O. (Ornamentum) coriaceus. Hoogstraal (1956) reviewed the biology of the species. It is found throughout Africa, the Middle East and India. Its distribution is strongly correlated with those areas that use dromedary camels. It is found in shaded areas where animals are tethered or at rest. It is not usually found indoors. It normally rests under the sand surface from which it emerges to feed at night. It is not normally associated with any disease but can maintain Borrelia crocidurae (Leger) (Gaber et al., 1984) and transmit ASFV experimentally (Mellor and Wilkinson, 1985). Ornithodoros (O.) savignyi, with its wide host range, including pigs, and its presence in ASFV endemic areas, suggests it may be a natural field vector of this disease (Mellor and Wilkinson, 1985).

Ornithodoros (O.) coriaceus, originally a deer parasite in California, has long been associated with the cattle disease, epizootic bovine abortion. A number of viral agents and a clamydial agent have been isolated from the tick but were not responsible for the disease (Storz et al., 1960; McKercher et al., 1969, 1973, 1980; Wada et al., 1976; Schmidtman et al., 1976).

Finally, a spirochete was isolated that is transmitted by bite or via coxal fluid but does not cause infections in mice or rabbits and can only be detected in the tick or cultures of tick tissues (Lane et al., 1985). Osebold et al. (1986) demonstrated that the spirochete discovered by Lane and his colleagues is the cause of the disorder. Additionally, in northern California, O. (O.) coriaceus transmitted a mild strain of C. burneti (Enright et al., 1971).

In Australia, the kangaroo tick, Ornithodoros (P.) gurneyi, is a parasite of crepuscular macropods, especially the red kangaroo, Macropus rufus (Desmarest). The ticks are found in loose soil in kangaroo wallows in open savannahs. Doube (1975a,b) examined its biology in the laboratory. The larvae, unlike other Pavlovskyella, remain attached for four to six days and nymphal instars one, two and three also remain attached for several days. The species also undergoes a reproductive diapause when exposed to low (10-15°C) or high (40°C) temperatures or short photoperiods. No diseases are known to be associated with this tick and it is not a livestock pest.

The genus Otobius, with its specialized life cycle, is the most highly evolved Argasid genus toward a free living life style. There exist few diseases associated with these ticks beside the fact O. megnini has become a problem in

cattle worldwide where it may occlude the ear canal and cause severe irritation and discomfort. Cases of human parasitism have also been reported and even a case of human paralysis due to the presence of a nymphal Otobius megnini in the ear of a South African child (Peacock, 1958).

Colorado tick fever virus was isolated from Otobius lagophilus parasitizing infected rabbits in Nevada and Utah (Berge, 1975; Hoogstraal, 1985). This disease is primarily associated with Dermacentor andersoni Stiles and the impact of this argasid/virus cycle on the epidemiology of this disease is unclear. Also unclear is the importance of this tick in the transmission cycle of Rocky Mountain spotted fever.

Interactions of Argasid Ticks with the Wider Environment

As can be seen in the previous section, argasid ticks are found in a wide variety of habitats, parasitizing a variety of animals and can transmit many disease causing agents. The conventional wisdom is that argasid ticks cause problems only in small localized areas and their impact to man is only minimal. This belittling attitude is true in most cases, but not all. The potential problems that these ticks could cause has been demonstrated in a few cases only, but they show the fallacy of classifying the Argasidae as esoteric, unimportant pests.

In some cases, man's activities have generated the opportunity for argasid tick transmission or the expansion of a minor zoonotic argasid into the sphere of man's activities where it has become a pest. Examples of zoonotic disease transmission impacting on man include epizootic bovine abortion in cattle exposed to the deer parasite, O.(O.) coriaceus, or relapsing fever transmission by O.(P.) hermsi in mountain cabins (Schmidtman et al., 1976; Harwood and James, 1979). Man's activities are no doubt responsible for the spread of the pests: Otobius megnini, Argas (P.) persicus and Ornithodoros (A.) lahorensis. Man's activities have also provided habitats for some of the more adaptable parasites which then became pests. Examples include Ornithodoros (P.) maroccanus and O.(O.) moubata in pigsties (Hoogstraal, 1985), the chicken coop parasitizing Argas (Persicargas) spp. and O.(P.) rudis and O.(A.) boliviensis into Latin American houses (Cooley and Kohls, 1944).

Global transport of diseases is a significant problem and is accomplished both by man and by ticks themselves. Three argasid vectored diseases transported internationally by man are African swine fever, aegyptianosis and avian borreliosis (Hoogstraal, 1985). The international transport of argasid tick diseases by ticks themselves was recognized by Hoogstraal (1961) with migrating birds that

carried ticks. Pelagic bird migration is no doubt responsible for the distribution of the Ornithodoros capensis species group and the viruses in the Hughes serogroup. Bird migrations and colonization, such as that of the cattle egret, Bulbucus ibis (L.), from Africa to the Americas, if involving infected birds could expose local argasids to a foreign virus like Qaranfil.

Man's recent broad scale exportation of exotic fauna to other continents, whether legally or illegally, could introduce foreign argasid ticks. The potential for this problem is well demonstrated by the international movement of domestic animals and its subsequent effect.

As has been shown, soft ticks provide a suitable environment for the culture and vectorship of a wide variety of pathogens. Therefore, new pathogens introduced into its nidus have the possibility of survival and future transmission. Additionally, the long life of argasids could provide a maintenance reservoir for a pathogen. When the tick vectors the pathogen it may then spread widely via more mobile vectors such as mosquitoes. Examples of this system are the Qaranfil virus and West Nile virus in Egypt (Hoogstraal, 1985). Another opportunity for disease interaction between argasid species and nidi can occur where they are adjacent geographically. This allows an animal, infected by the bite of one tick, to be fed upon by

another species of tick for which it is an abnormal host-- thus infecting both tick species. An example of this is Caspiy virus found in both O.(A.) coniceps and O.(A.) maritimus (L'vov et al., 1980).

Any or all of these epidemiological factors could interact to generate a new epidemiological problem that would showcase soft ticks as significant vectors--just as African swine fever has done recently in Spain and Portugal. That experience should serve as a warning for disease epidemiologists and entomologists to not forget the vector potential of members of the family Argasidae.

CHAPTER III MATERIALS AND METHODS

Sites

Field ecological study sites were selected to study the ecology and bionomics of Ornithodoros t. americanus in two habitat types. The two sites selected were concurrently being used for gopher tortoise ecological studies by Joan Diemer, a researcher for the Florida Game and Fresh Water Fish Commission, for research on gopher tortoise ecology. The use of these sites provided a large database on the history of each burrow and tortoise present.

The first site was on the Lochloosa Game Management area in southeastern Alachua Co. (N 29° 31' 10" - W 82° 11' 10"). The tortoise burrows used were on both sides of a 0.5 km stretch of hard packed dirt road through a plantation of slash pine, Pinus elliottii Engelm. Most burrows were constructed in the soil banks created during the road's construction. The site had a moist dark soil. The water table was estimated at no more than 1.5 meters below the soil surface.

The second site was located several miles north of Hollister in Putnam Co. (N 29° 41' 40" - W 81° 48' 10") on a piece of property known as Robert's ranch. The site was located on the top of a typical sandhill. The overstory

vegetation on the site consisted of a mix of longleaf pines, Pinus palustris Mill (=australis), turkey oak, Quercus laevis Walt., scrub live oak, Quercus geminata Bdv., and post oak, Quercus stellata Wang var. margaretta. The understory was mostly wire grass, Aristida stricta Michx. with some palmetto, Serenoa repens (Bartram) Small and numerous herbs. The soil was of the Norfolk type and the water table was at least three meters below the soil surface. More in-depth descriptions of typical sandhill vegetation and soils is available in Kurz (1942) and Laessle (1958).

Burrows

Gopher tortoise burrows selected for sampleable lengths of at least 3 meters. At the Lochloosa site 15 burrows were selected from 27 available. At the Robert's ranch site 30 were selected from 43 tested. This restriction limited data collection to those burrows made by large juveniles or adult gopher tortoises. Most burrows were "active," i.e., occupied, at the start of the study.

Collections at Lochloosa were separated over two weeks and at Robert's ranch over three weeks. There were 10 sampling periods at each site from June 19, 1984, to November 15, 1985.

Sampling Technique

The sole sampling technique used in this study was vacuum extraction. The machine used for extraction was a modified version of the "Tick Sucker Mark V" described by Butler et al. (1984b). The main modification to the Echo R200 power blower (Kioritz Corp., Toyko, Japan), besides the use of a metal impeller, was the collection apparatus.

Attached to the back of the machine, over the impeller intake was a metal inverted L-shaped baffle. The dimensions of the vertical portion were 23 cm x 23 cm x 3.5 cm with the area over the impeller cut out. The base of the L projects away (10 cm) from the back of the machine. Within the baffle, a heavy gauge copper screen was added to protect the impeller from vacuumed debris. The inner portion of the L, the part facing the ground, was cut away and a seating flange and a pin hinge adapter was added. Suspended from the inner surface of the L base was the collection box. The collection box was made of steel (26 cm x 16 cm x 9 cm) with one end hinged and the other end with a latch for attachment to the air baffle (a modified ammunition box). This new system constructed by J.F. Butler was called the Tick Sucker Mark VI.

The vacuumed air and debris was drawn up a 4 cm (id) Super Vac-u-flex crushproof hose (Automation Industries, Inc., Flexible Tubing Division, Abbeville, SC) through a

fitting in the baffle box. The sand and other heavy material in the decreased vacuum pressure in the collection box separated out, whereas the light leaves were trapped in the copper guard screen. The S-shaped baffle air flow design allowed quantitative samples of materials from the burrows to be taken using a portable machine while still protecting the motor and impeller.

Burrow sampling was done by feeding the hose into the hole until it could not move any further forward, either due to an obstruction or the end of the length of hose (5.5 m). The hose was then attached to the machine and the machine turned on. As the hose was pulled out of the hole (rate = 15 sec/m), it was pushed back and forth and twisted to increase vacuumed area. If the hose became blocked, the depth and time were noted and, after clearing, vacuuming was resumed at that depth and time. If vacuumed samples were below 500 cc the run was repeated. Three vacuumed samples were taken from each burrow and noted in sequential order. All samples were kept in Ziplock^R 1 gallon plastic bags and transported in styrofoam or plastic coolers to the laboratory for separating and evaluation.

Sorting

Sorting required separation of materials by sifting out the invertebrates from the sand. Two sifting bags made

of plastic screening were used (large gauge 6 threads/cm; small gauge 13 threads/cm). If the soil samples were to wet to sift, they were dried on trays placed upon the warm surface of a Salton Hottray automatic food warmer Model H-160-D (Salton International, New York, NY).

All Ornithodoros ticks collected from each sample were kept alive in plaster of paris filled 25 ml plastic vials with fine screened tops (Beck et al., 1986). All other invertebrates were placed in alcohol for preservation unless kept for rearing. After counting and marking, ticks were returned to the burrows from which they were collected, usually 7 days after collection. Some blood fed ticks were kept for blood meal identification.

All Ornithodoros ticks were maintained under the environmental conditions used by Beck et al. (1986). Observations of O. t. americanus behavior was done in the Hotpack chamber (Hotpack Corp., Philadelphia, PA) using an F₁ laboratory colony kept in an 10 gallon glass aquarium. The aquarium had approximately 10 cm of glass beads, ca. 0.5 mm diameter, in the bottom. Security was maintained by the use of a 100 watt resistor heating element maintained at 60°C by a Versa-Therm temperature controller (Cole Palmer Instruments Co., Chicago, IL) around the top of the tank which repelled the ticks.

Fluorescent Marking

For a Fisher-Ford mark-release-recapture population estimate of the tick population (Begon, 1979) a permanent marking system was needed. Fluorescent dyes have been used with Argas radiatus (Medley and Ahrens, 1968,1978) and dusts with Ornithodoros turicata (Adeyeye, 1982).

Day-glo fluorescent pigments (Day-Glo Color Corp., Cleveland, OH) were selected for permanent marking of ticks. Direct coating with the dust was found to affect the tick adversely, with small percentages of them bloating and dying. Minute glass beads or sand was used as a carrier for the dust and provided an even coat, with no obvious mortality. The colors used were: Saturn Yellow, Blaze Orange, Rocket Red, Horizon Blue, Signal Green. Other colors were produced by mixing pigments: Mix 1 (Horizon Blue:Rocket Red, 1:1), Mix 2 (Signal Green:Rocket Red, 1:1), Mix 3 (Horizon Blue:Signal Green, 1:1) and Mix 4 (Horizon Blue:Saturn Yellow:Blaze Orange, 1:1:1). Each produced a distinct color, observable in normal or ultraviolet light.

A desk lamp fitted with a magnification glass and two 366 nm ultraviolet fluorescent light bulbs was used to identify the marked and unmarked naturally fluorescing ticks (Adeyeye, 1982; Butler et al., 1984b).

Temperature and Humidity Measurements

Temperature and relative humidity measurements were taken using either a sling psychrometer (J.L. Stortz Div., PSG Industries Inc., Perkasio, PA) or a Vaisala electronic humidity and temperature indicator HMI 31 (Vaisala Corp., Finland). Amounts of soil water were measured by taking approximately 50 g of a sample and measuring the difference between wet and oven dried soil and converting it to a percentage of soil weight. Oven drying of the soil took 48 hours at 120°C.

Age and Sex Structure of Tick Populations

Using laboratory reared stock for comparison the size range of field collected N_1 , N_2 and N_3 ticks were estimated. The older nymphal stages had size ranges too variable to use. A reference template, made of balsam preserved ticks showing the size range of these stages, was used to identify the nymphal stage of field collected material. Larvae were distinguished by their three pairs of legs. Adults were easily identified by the presence and structure of their reproductive orifices.

Blood Meal Identification

Tick blood meal identification was by the use of Ouchterlony immunodiffusion precipitant tests. Crushed

blood fed field collected ticks were tested against polyclonal antisera to most of the burrow inhabitants. The Ouchterlony immunodiffusion plates used were made from Agarose Immunodiffusion Tablets (Bio-Rad Laboratories, Richmond, CA) and the gel was poured on to standard size microscope slides seated in Gelman immunotrays (Gelman Instrument Co., Ann Arbor, MI). Added to the 1% agarose gel in 50 mM NaCl, 50 mM HCl Tris buffer, pH 7.2, several drops of bromophenol blue was added to improve visibility of precipitated bands. Two plates of 9 wells each were cut in each slide using a Gel punch (Gelman Instrument Co., Ann Arbor, MI).

Antiserum was developed against the following species: southern leopard frog, Rana sphenocephala Cope (cross reacts with gopher frog, Rana areolata aesopus Baird and Girard); gopher tortoise, Gopherus polyphemus; eastern diamondback rattlesnake, Crotalus adamanteus Beavois (cross reacts with most snakes); eastern grey squirrel, Sciurus carolinensis Gmelin (probably cross reacts with fox squirrel, Sciurus niger Linnaeus); deer mouse, Peromyscus maniculatus (cross reacts with Florida mouse, Peromyscus floridanus (Wagner)); raccoon, Procyon lotor; opossum, Didelphis virginiana; armadillo, Dasypus novemcinctus; and mixed bird (chicken, quail, dove, grackel, cardinal and bluejay).

The antisera was produced in New Zealand white rabbits. Known blood sera was emulsified with equal parts Freund's complete adjuvant (Difco Laboratories, Detroit, Mich.) and injected subcutaneously into the rabbits near the lymph nodes of the leg joints. The protocol, designed by Dr. S. Zam, was as follows: week 1 - 1/4 ml of mix in each foreleg, week 2 - 1/4 ml in each hindleg, week 4 - 1/4 ml in each leg, week 6 and week 8, harvest 50 ml of blood via ear bleeding. Immunoglobulin purification was done by protein precipitation of the rabbit sera. Three sequential precipitations of 50%, 30% and 30% (by volume) of saturated ammonium sulfate (pH 7.2) were done. The final precipitant was redissolved in phosphate buffered saline and placed in an osmosis bag to eliminate any residual ammonium sulfate.

All rabbits used showed no Ouchterlony immunodiffusion precipitant reaction to the test animal sera or tick body fluids prior to their being used for antisera production. All antisera produced were found to be highly specific for the animal species sera used. No cross reactions in Ouchterlony plates were seen between any antisera and the other host sera used for antisera production. Cross reactions were seen in the Peromyscus antisera for several Peromyscus species but not to species in other mouse or rat genera. The snake antisera cross reacted with coral snake, rattle snake and all Colubrid species tested but not to

lizard or tortoise sera. The frog antisera cross reacted with Rana species but not Bufo or other frogs or toads. All other antisera produced showed no cross reaction to other burrow inhabiting species. Antiseras were not produced for other known burrow inhabitants such as the several toad and lizard species. The antiseras produced were highly sensitive and would still precipitate host sera antigens on Ouchterlony plates in the 1:32 to 1:128 dilution range.

The Ouchterlony immunodiffusion plates were loaded with the antiseras in the outer wells and fluids from the crushed blood fed tick in the central well. The plates were allowed to diffuse for 48 hours before being read. The slides with the ouchterlonys were soaked in saline overnight, dried and stained with the Crocein scarlet stain of Crowle and Cline (1977) to confirm a correct reading. They were then able to be redried and stored for future reference.

Invertebrate Identification

Identification of field collected invertebrates to the family level was generally made by the author. Genus and species identification unless specified otherwise were also made by the author. Species level determinations for the remaining groups were made by the following experts:

Snails--Dr. Kurt Auffenburg, Florida State Museum; spiders, centipedes and millipedes--Dr. G.B. Edwards, Florida Division of Plant Industries (DPI); chiggers--Dr. W.J. Wrenn, University of North Dakota; fur mites--Dr. A. Fain, Institut Royal des Sciences Naturelles de Belgique; Oribatid or beetle mites--Dr. R. Norton, SUNY College Environmental Science and Forestry; Hemiptera--Dr. F. Mead, DPI; antlions--Dr. L.A. Stange, DPI; Staphylinidae or rove beetles--Dr. H. Frank, University of Florida; Scarabaeidae or scarab beetles--Dr. R. Woodruff, Florida Division of Plant Industries (DPI); Ptomophagus beetles--Dr. S.B. Peck, Carleton University; Lepidoptera and all larvae--Dr. D.H. Habeck, University of Florida; Acrolophidae--Dr. D. Davis, Smithsonian Institute; Mycetophilidae--Dr. J.R. Vockeroth, Biosystematic Research Institute, Agriculture Canada (BRI-AC); Sciaridae--Dr. A. Borkent, BRI-AC and Dr. R.J. Gagne, USDA-ARS-SEL; Therividae--Dr. M.E. Irwin, Illinois Natural History Survey; Asilidae--Dr. S.W. Bullington; Phoridae--Mr. B. Brown, University of Alberta; Sphaeroceridae--Dr. S.A. Marshall, University of Guelph; Drosophila--Dr. M. Wheeler, University of Texas at Austin; Milichiidae and Chloropidae--Dr. C.W. Sabrosky, USDA-ARS-SEL; parasitic Hymenoptera (families)--Mr. R. Prage, University of Florida; and ants--Dr. J. Trager, University of Florida.

Dr. R.E. Woodruff's 1982 article on arthropods of gopher burrows was also extremely helpful in identification.

Calculations and Statistics

Data management and statistical calculations were carried out on an IBM PC-XT. The computer program Lotus^R (Lotus Development Corp., Cambridge, MA) was used for data management and for the Fisher-Ford population estimate. NWA Statpak^R (Northwest Analytical, Portland, OR) was used for Student's t-tests and analysis of variance calculations. An IBM Basic program developed by A.F. Beck was used to calculate a population estimate based upon the removal sampling estimation formulae of Carle and Maughan (1988).

CHAPTER IV RESULTS AND DISCUSSION

Animals Present at the Site

In the habitats of the gopher tortoise there are a number of other vertebrates. Some are associated, to a greater or lesser degree, with the gopher tortoise burrow and a few just utilize the general habitat. During the course of the study a number of animals were identified as using the burrows. Identification was based upon capturing them in the burrow or by recognition of their tracks entering or leaving the burrows. Those animals and their frequency of observation are listed in Table 4-1. With the exception of the spadefoot toad, all species listed have been reported previously (Hallinan, 1927; Moore, 1953; Eisenberg, 1983; Humphrey et al., 1985; Franz, 1986a, personal communication).

Snakes were not captured or flushed from burrows, however snake tracks in and out of the burrow were frequently seen and shed skins of Colubrids (non-poisonous snakes) and Crotalus (rattlesnakes) were occasionally collected in burrow vacuum samples. At the Roberts ranch site Eastern diamondback rattlesnakes, Crotalus adamanteus; Eastern coral snakes, Micrurus f. fulvius (L.); Eastern indigo snakes, Drymarchon corais couperi (Holbrook) and

Table 4-1. Vertebrates that are known to utilize the burrows constructed by gopher tortoises at the two sites.

<u>Common Name</u>	<u>Scientific Name</u>	<u>No. of Observations/site</u>	
		<u>Flatwoods</u>	<u>Sandhill</u>
gopher tortoise	<u>Gopherus polyphemus</u>	20+	20+
Florida gopher frog	<u>Rana areolata sesopus</u>	20+	4
Florida mouse	<u>Peromyscus floridanus</u>	---	20+
opossum	<u>Didelphis virginiana</u>	9	2
armadillo	<u>Dasypus novemcinctus</u>	5	3
Southern toad	<u>Bufo terrestris</u>	3	3
six-lined racerunner	<u>Cnemidophorus s. sexlineatus</u>	2	2
green anole	<u>Anolis carolinensis</u>	---	2
raccoon	<u>Procyon lotor</u>	1	2
fox squirrel	<u>Sciurus niger</u>	---	2
cotton mouse	<u>Peromyscus gossypinus</u>	2	---
ground skink	<u>Scincella laterale</u>	2	---
Florida cricket frog	<u>Acris gryllus dorsalis</u>	2	---
fence lizard	<u>Sceloporus u. undulatus</u>	---	2
Eastern narrow mouthed toad	<u>Gastrophryne carolinensis</u>	1	---
Eastern spadefoot toad	<u>Scaphiopus h. holbrooki</u>	---	1

black racers, Coluber constrictor Dunn and Wood, were seen. At the Lochloosa site diamondbacks, black racers and garter snakes, Thamnophis s. sirtalis (L.) were present. All of these species are known to frequent the burrows (Hallinan, 1927; Franz, 1986a). Besides these species, Franz (1986a) captured five more snake species in burrows and two lizard species not encountered in this study.

Four additional mammals present at the sites were involved with burrows, but their impact was generally negative. Collapsed burrow entrances were generally caused by white tailed deer, Odocoileus virginianus Zimmermann, or cattle (Lochloosa only) walking across the top of the entrance. Black bears, Ursus americanus Pallas, twice at Roberts' ranch, and a dog at Lochloosa, attempted to dig out the tortoises and enlarged or obliterated the entrances. At a number of sites not used during this research, dogs have been known to dig out as many as 30% of the entrances. Foxes also enlarge gopher tortoise burrows for use as dens (Eisenberg, 1983).

Four birds present at the site were observed to forage near or on the burrow entrance skirts so that some may contact ticks from the burrow. These species were: Towhee, Pipilo erythrophthalmus (L.); bobwhite quail, Colinus virginianus (L.); wild turkey, Meleagris gallopavo L.; and pinewood sparrows, Aimophila aestivalis (Lichtenstein).

Wild swine were never seen at either site. No evidence of their rooting behavior was seen. Despite the fact that two dirt roads transect the sites and plenty of open sand areas were present throughout both sites, no tracks of swine were observed. This is surprising since in the general vicinity of the sites these animals were common.

Feral swine have been investigated extensively by the Wildlife Research Laboratory, Florida Game and Fresh Water Fish Commission. In a report by Belden et al. (1985) the feeding habits, growth and population structure of feral swine were discussed. Belden (personal communication) stated that wild hogs primarily are found in swamp and mesic hammocks and that hogs rarely occur in habitats in which gopher tortoises reside. This conclusion is further substantiated by Greiner et al. (1984) who found neither Ornithodoros turicata nor larvae or nymphs of Amblyomma tuberculatum Marx, the two gopher tortoise burrow parasites, on any of the 645 feral swine examined. This evidence suggests that feral swine encounters with Ornithodoros t. americanus would be very rare.

However, in certain instances gopher tortoises and hogs do coexist. In the Fisheating Creek Wildlife Management area both exist on the site but soft ticks were not present in the burrows (Beck and Gibbs, unpublished

records). In swamps, gopher tortoises can be found on mesic hammocks Beck, unpublished data). These areas are prime habitats for swine and so although tick encounters may be rare it is feasible that ASF could develop an endemic feral foci in Floridian tick populations.

Adeyeye (1982) found that ticks came out onto the entrance skirt more commonly at night than during the day. This is significant since tick/swine interaction must occur when ticks are out of the burrow. Wild swine however, have diurnal and nocturnal foraging behavior patterns (Singer et al., 1981), so they are unlikely to remain in the vicinity of a gopher tortoise burrow entrance long enough for the tick to locate and feed on the pig and then succeed in returning to the security of the burrow.

In domestic situations however the potential interaction of O. t. americanus and swine is probably greater. Adeyeye (1982) demonstrated that the tick would feed on domestic swine and that they would parasitize caged piglets 2 meters from a burrow entrance. Swine can be found on many farms in Florida where gopher tortoises, and presumably O. t. americanus, are present. Despite the fact that Boardman (1929) and Clements (1956) do not report gopher tortoise parasites on domestic swine, two collections of Ornithodoros turicata from swine and "sinks frequented by pigs" by T.W. Cole in Suwannee and Marion

County, Florida were reported (Cooley and Kohls, 1944). So the infection of Ornithodoros t. americanus with African swine fever virus probably would occur through infected swine exposure on rural farms. Additionally, the infection of unexposed swine by the feeding of previously ASFV exposed Ornithodoros ticks has a higher probability of occurring in the domestic rather than in the sylvatic situation because of higher densities of pigs and the induced proximity of pigs to an infected burrow nidus.

This evidence suggests that on rare occasions Ornithodoros t. americanus will be found associated with swine. Due to the difficulty in obtaining blood fed ticks, the short period of time that a blood meal is identifiable and the probable localized nature of swine/tick interactions, the examination of soft ticks is unlikely to clarify this epidemiological problem. The current development of a monoclonal test and improvements in the collection of tick antigens under the direction of Drs. J.F. Butler and S.C. Zam are designed to detect the amount of tick antigens or anti-tick antibodies in the blood of swine. These tests, when developed, could be used to measure the amount of swine/tick interaction both in wild swine and domestic hogs.

The three mammals that infrequently utilize the burrows are raccoon, opossum and armadillo. Eisenberg

(1983) states that opossums use the burrows for shelter from the midday heat. Eisenberg (personal communication) and my observations suggest that the armadillo and the raccoon enter burrows while foraging for food and presumably do not remain for long periods. The Eastern cottontail rabbit, Sylvilagus floridanus Aller, was present at both sites, and has been reported to use burrows as a refuge (Hallinan, 1927), but no evidence of this was revealed during this study.

The two other mammals encountered, the fox squirrel and the Florida mouse used gopher burrows as nest sites. The fox squirrel sightings at Robert's ranch were in an inactive burrow where a leaf nest was constructed. This activity was previously reported by Moore (1953). The Florida mouse is a burrow commensal whose behavior and distribution is bound to that of the gopher tortoise. At the Robert's ranch site 26 of the 30 burrows had a mouse or two living in them, at least once during the course of the study. Extensive research on the Florida mouse has been reported including habitat preference, density, development, behavior and parasites (Layne, 1963; King, 1968; Eisenberg, 1983). The cotton mouse observations also involved nesting. Unlike the Florida mouse whose nest is constructed in a side burrow (Eisenberg, personal communication), the cotton mouse nest was constructed in

the main burrow. The cotton mouse nest was found placed in an abandoned burrow about 2.75 meters from the entrance.

The last mammal to be considered is the pocket gopher, Geomys pinus Rafinesque. This subterranean rodent constructs elaborate burrow systems in the same habitat as the gopher tortoise (Brown and Hickman, 1973). Their behavior is reminiscent of a large mole. No published evidence describes a connection between its burrow system and any active or inactive gopher tortoise burrow, but it may occur. If it does occur, the tick parasites may crossover. Hubbell and Goff (1940) do not report any invertebrate species crossover or the presence of soft ticks in the burrows, but their studies did not involve extensive excavation. Whether pocket gophers serve as alternate hosts for Ornithodoros t. americanus should be considered an unanswered question.

Although not present at either study site, the burrowing owl, Athene cunicularia constructs its nests in burrows and Ornithodoros t. americanus, has been collected in these burrows (Milstrey, 1986). The importance and suitability of this host is suspect because in the two cases of positive reports by A. Beck at Marion County, Florida, gopher tortoise burrows were also present. At two separate owl colonies in Lake County, Florida, with no gopher tortoises present at the site for 5 years, this

author collected no ticks. Similar negative results were reported at three other burrowing owl sites in Dade and Broward Counties, Florida, by A. Beck and R.C. Wilkerson (unpublished data). Further studies on the role of this bird species on the maintenance and dispersal of Ornithodoros t. americanus should be done.

Florida mice use tortoise burrows as shelters to escape environmental adversities and as places to reproduce and raise their young (Eisenberg, 1983). Similarly, Franz (1986b) believed that the gopher frog and the Florida pine snake depended on these shelters to escape the adverse external conditions and certain predators. This is likely to be true for most of the other amphibians and reptiles that utilize the burrow.

The burrows also serve as a forage site for these animals. Fecal extracts of Florida mice and stomach contents of gopher frogs revealed that they used the commensal insects as part of their diet. Laboratory observations confirm their willingness to feed on the insects present. Florida mice ate all commensal beetles and insect larvae they were offered. The mice did not attack flies, spiders or the beetle, Ptomophagus texana Melander. Florida gopher frogs preferred the flies and Ceuthophilus crickets. Similar predation presumably occurs with and between the other vertebrates present, as it seems

unreasonable that the burrows serve as "neutral territory" in the struggle for survival.

Blood Meal Identification

A summary of the results of the tick collections and blood meal analyses for the two sites are presented in Tables 4-2 and 4-3 and Figures 4-1 and 4-2. Over 10,000 ticks were collected during the course of this investigation. At the Lochloosa Game Management Area site there were only 16 holes sampled compared to 30 at the Robert's ranch site. Based upon the number of ticks collected at each site, 3.5 times as many ticks were collected per hole at Lochloosa verses those at Robert's ranch. It was also more likely that those ticks collected at Lochloosa would be fed. In the Lochloosa samples, 7.2% of the population was fed compared to 4.4% at Robert's ranch.

The Lochloosa results are misleading. During one collection period, at one hole, 240 of 341 ticks collected were fed. Of the ticks collected, 82.1% were larvae, and of those 94.6% were fed. So if this observation is deleted, the percentage total ticks fed is 3.9%, not 7.2% and percentage of larvae fed is 2.2% instead of 9.0%. Comparisons of relative numbers fed in each stage collected at Lochloosa and Robert's ranch are presented,

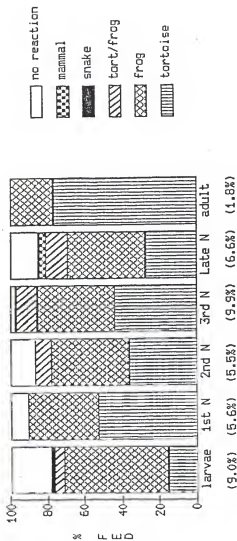
Table 4-2. Summary of results of the blood meal analyses on field collected Ornithodoros (p.) t. americanus at the Lochloosa flatwoods site.

	All Stages	Larvse	Nympha			Female	Male
			1st	2nd	3rd		
Total ticks captured	6931	3252	1199	821	515	209	494
Fed ticks captured	503	293	67	45	51	8	10
Fed ticks analyzed	239	77	53	36	34	4	9
Tortoise	85	12	28	13	15	3	7
Frog	106	43	20	15	14	1	2
Tortoise & frog	14	4	0	3	4	0	0
Snake	1	1	0	0	0	0	0
Opossum & tortoise	1	0	0	0	0	1	0
No reaction	32	17	5	5	1	4	0

Table 4-3. Summary of results of the blood meal analyses on field collected Ornithodoros (P.) t. americanus at the Robert s ranch sandhill site.

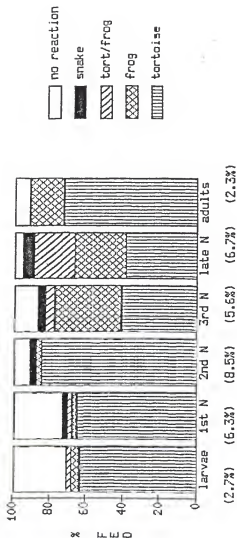
	All Stages	Larvae	Nymphs			Female	Male
			1st	2nd	3rd		
Total ticks captured	3650	1529	588	386	396	148	333
Fed ticks captured	163	41	37	33	22	6	6
Fed ticks analyzed	162	41	37	32	22	6	6
Tortoise	101	26	24	27	9	4	4
Frog	20	2	1	1	8	2	1
Tortoise & frog	8	1	1	0	1	0	1
Snake	4	0	1	1	1	0	0
Mammals	0	0	0	0	0	0	0
No reaction	29	12	10	3	3	1	0

Figure 4-1. Blood meal analyses of Ornithodoros t. americanus at the Lochloosa pine flatwoods site. Percentages that each host contributed to the total number of meals analyzed for each stage.



STAGE OF DEVELOPMENT

Figure 4-2. Blood meal analyses of Ornithodoros t. americanus at the Robert's ranch sandhill site. Percentages that each host contributed to the total number of meals analyzed for each stage.



STAGE OF DEVELOPMENT

respectively. Lochloosa results in which the unusual occurrence is deleted are given in parentheses. The percentages are for larvae, 9.0%, (2.2%), 2.6%; first nymph, 5.6%, (4.9%), 6.3%; second nymph, 5.5%, (5.4%), 8.5%; third nymph, 9.9%, (9.6%), 5.6%; late nymph, 6.6%, (6.6%), 6.7%; females, 1.9%, (1.9%), 3.4%; and males, 1.8%, (1.9%), 1.8%. So at Robert's ranch a collected tick of any stage is more likely to be fed than those at Lochloosa (α error = 0.45). This analysis negates the heavy bias toward larvae inherent in a percentage derived from a summation of data for all stages.

In the sandhill site, blood meal analysis shows that the predominant host was the gopher tortoise. At Lochloosa, where gopher frogs were common, there were more blood meals from this frog than from gopher tortoises. Only five gopher frogs observations occurred at the sandhill site compared to more than twice that number at the Lochloosa location.

This demonstration of O. t. americanus feeding on the gopher tortoise is the first such account published. Joan Diemer in her trapping of tortoises in the field has on rare occasions collected engorged specimens from tortoises. This includes not only mature tortoises, but also freshly hatched ones (Diemer, unpublished data). A second hand

report, attributed to Jim Layne of the Archibold Biological Station in Highland County, Florida, said that the ticks were found to parasitize tortoises at their research site. Ticks feeding on tortoises were most commonly collected from between the scutes on the carapace. Careful examination of tortoises when they are not retracted within their shell sometimes yielded a tick feeding at the margin of the carapace and skin. Only on a hatchling tortoise was feeding observed through the skin covering the extremities, in this case, the neck region. In adult tortoises the skin is horny and thick and difficult to penetrate even with a surgical needle, so tick feeding attempts in these regions would be difficult.

Hubbard in 1894 stated that he collected Ornithodoros americanus from tortoises, but he retracts this statement in 1896 (Hubbard, 1896). There are two other references that do mention Ornithodoros parasitism on Gopherus sp., however they were for the desert tortoise, Gopherus agassizii (Cooper), in California. Both O.(P.) turicata and O.(P.) parkeri were recovered (Harbinson, 1937; Ryckman and Kohls, 1962) and the reports state that these western populations of ticks parasitize the tortoises in the same locations on its body as observed on the Florida gopher tortoise.

In burrow samples with tortoise fed ticks, some ticks would be plump and give every appearance of being fed, but they would not have the reddish color of a blood fed tick, instead they were the normal sand color or yellowish. These ticks were predominantly younger ticks, early nymphs or larvae. When tested by immunodiffusion these specimens gave very strong positive reactions to tortoise antisera. They had feed on tortoise but recieved no red blood cells, just serum. It was found that in the membrane between the scutes of the tortoise the capillaries were so fine that skin scarification yielded only serum. All serum fed specimens tested positive for tortoise. So if a serum fed specimen was collected it probably indicated that a tortoise was or had recently been present in that burrow. Laboratory data moderates this conclusion since serum feedings were infrequently encountered during maintenance feeding on other hosts.

Gopher frogs were frequently encountered during the research. Four of the nine captured frogs (44%), had Ornithodoros t. americanus attached. Four southern toads were captured. On one toad 2 O. t. americanus ticks were attached, one first nymph near the neck region and the other on the belly. The numbers of ticks per parasitized frog were 1, 2, 5 and 11. Dick Franz trapped large numbers of these frogs on the Ordway Preserve in Putnam County and

found in some cases an excess of 20 ticks on a single frog (Franz, unpublished data).

Preferred attachment sites on the frog were on the belly, hind legs, lower back and more uncommonly the forelegs and thorax. Ticks were never observed on the upper back or head of the frog. These feeding sites are probably not selected, but fortuitous, since these are the areas of the body that comes in contact with the sand substrate as the frog sits against the wall inside the burrow. One frog collected at another site in Newberry, Alachua County, had 6 ticks attached and they were placed in a ring around the belly and lower back. This became apparent as the frog sat on a sand substrate so that all the attached ticks were located at the surface of the sand.

Although the southern toad is a new host record for the tick, the gopher frog is not. Boardman (1929) reported that he had "taken 3 specimens on the gopher frog which inhabits the tortoise burrow". Although the local was not specifically mentioned, he stated previously that specimens were collected near Gainesville (Alachua County, FL). Since this report no other corroborative evidence had been reported.

Snakes served as blood sources for ticks on five occasions; once at Lochloosa with a larval tick and four times at Robert's ranch with nymphs. No adult collected

ticks showed any snake blood meals, however laboratory studies show that adults will feed on rattlesnakes, digest the meal and produce viable eggs. The 1 to 4 ratio of snake fed ticks from Lochloosa as compared to Robert's ranch seems to reflect the frequency of snakes encountered at both sites. All five burrows where the single snake fed ticks were collected were either inactive or abandoned. Whether snakes actively select burrows without tortoises present can perhaps be answered by more extensive examination of Franz's collection data (Franz, 1986a). If so snakes could provide an additional way for a tick population to survive until a tortoise or frog returns.

Blood samples from 3 Florida mice at Robert's ranch site and 1 from a mouse captured at Ordway Preserve, by Cheri Jones of the Department of Zoology, were obtained during toe clipping. These samples were tested by Ouchterlony immunodiffusion against crude extracts obtained from several macerated anterior body sections of lab reared Ornithodoros t. americanus. In one of the Robert's ranch samples a faint band pattern was observed. In attempting to stain these bands (Crowle and Cline, 1977) they were lost. This was indicative, but not positive proof, that this mouse species is parasitized by the soft tick. More refined serological tests and the availability of pure tick salivary antigens may provide stronger proof.

Despite the fact that Florida mice were continuously present in many of the burrows at Robert's ranch, and a number of other mammals used the burrows at both sites, only one blood meal could be accurately attributed to any mammal, an opossum. In that case the meal, from the Lochloosa site, also contained tortoise blood.

A relatively high proportion of analyzed blood meals did not react with any of the test antisera, 18.1% from Robert's ranch and 13.4% from Lochloosa. The distribution of non-reactives was inversely correlated with size. The smaller the tick, the less likely the meal could be identified. Selection of blood-fed ticks was dependent upon their reddish-black appearance and their plumpness. Some ticks were selected solely on their plumpness since ticks feeding on gopher tortoises often only obtained serum, so their yellowish color did not change. During the course of the study it was found that some plump black ticks would in preparation for analyses be shown not to contain a fresh meal, but just a black gritty residue assumed to be digested hematin (Balashov, 1968). These ticks, especially small stages, would show weak or no precipitation reactions. The plump appearance may have been due to incomplete removal of excess fluid by the coxal glands, an advantage in dry conditions. Similarly, plump

black nymphal ticks, weeks after feeding, could be occasionally seen in the laboratory tick colony.

Another point that contributed to increases in numbers of non-reactive ticks was the lag period from collection through sorting to testing. This lag could be as long as 8 days with a mean of 3-4 days.

A laboratory study using cotton rats, Sigmodon hispidus, and cotton rat antisera showed that the serological detectability of a host failed before the "blood fed appearance" of the tick diminished. Larval meal identification fell to 60% by day 6 and 0% by day 9. By day 12, third instar nymphs and males showed a 66% and 75% positive response, respectively. Serological tests of post molt nymphs 24 days after feeding showed no positive serological reaction to the rats' serum proteins.

These data differ from the rates of digestion reported in O. (O.) moubata. In that species blood meal identification could be done up to a year later (Gozony et al., 1914; Weitz and Buxton, 1953). It appears the specimens used were adults since molting was not mentioned. In one of two male O. t. americanus, the meal could still be detected 60 days later.

Some ticks, that showed no reaction in the blood meal analyses, had fresh blood in their midguts. These meals should have reacted to the tests indicating the appropriate

antisera was not available for cross reaction. Antisera for all possible hosts was not available. These include also those hosts that do not enter burrows but may encounter ticks outside such as deer, man, cows or swine. One of these possible hosts that did not react with the antisera used, but was demonstrated to be a host, was the southern toad. Blood from this animal host and the engorged ticks collected from its body showed no cross reaction to the frog antisera or any other antisera. In some cases, blood meals were examined as giemsa stained smears. Most had nucleated erythrocytes, but three partially digested meals had erythrocyte-sized cells with no nuclei. It was not possible to conclusively distinguish these as mammalian blood cells or as non-mammalian erythrocytes "ghosts" produced during cell digestion.

One host category, shown on Tables 4-2 and 4-3, is tortoise and frog. This represents those ticks whose blood meals reacted to both tortoise and frog antisera. Only in 21 of the 449 burrow samples could the presence of both species be confirmed, thus the opportunity for identifiable multiple host meals are low. Multiple host feeding was found in all stages, except females. In those burrows with two hosts, multiple host meals represent 18.6% of those tested.

Host Preference

Multiple host feedings are very significant. The nearly 28% level of multiple host feeding signifies that this is a common occurrence. Although all stages of this tick species were found to multiple host feed, it became progressively more frequent in the nymphal stages. The following are the percentages of these multiple host feedings: larvae, 16% (n=41); first nymph, 3% (n=31); second nymph, 25% (n=12); third nymph, 24% (n=25) and late nymphs, 44% (n=18). This may relate to the longer digestion/molting time periods which would allow for more time to search for a host. During preliminary CO₂ attraction studies in 1981, at the Newberry site where Adeyeye (1982) did his research, several blood fed O. t. americanus were attracted from the burrow out onto the skirt along with unfed ticks. This provides support for the hypothesis that blood fed ticks will continue searching for hosts during its premolt period. Additionally, it should be realized that multiple feeding on the same species of host is impossible to detect by antisera cross reaction. Also, those fed ticks for which a single meal was identified does not necessarily mean it had only fed on one host species since additional host species may not have been detected due to not being tested for in the Oucuterlony

tests. This suggests that multiple feedings within a stage may be a normal occurrence for this species.

Buxton and Weitz (1953) state that they could serologically detect host blood even after another host species was fed in the interim before testing. Balashov (1968) in a cytological study of tick digestion found that female O. tholozani still retained semi-digested blood from the previous blood meal when they were ready to feed again. This provides evidence that in O. t. americanus adults it may still be serologically detectable to identify two hosts which were fed upon even when these attacks were separated by a long period of time. Either nymphal blood meals are completely digested prior to molting or after molting what little is left is undetectable. Although this evidence provides grounds to question multiple host feeding over a short time period in adults, the evidence for this behavior in nymphs is strong. In larvae, it is irrefutable since they had no prior meal.

The advantages of this behavior probably outweigh the costs for this species. The only disadvantage would be death due to host grooming and neither major host species exhibited such behavior. The advantage is that an individual tick can obtain more food per stage. Desiccation stress could also be avoided by more water available. Since more food can be obtained the subsequent

stage can be larger. Pound et al. (1986) have shown in the closely related O. (P.) parkeri that larger nymphal size is correlated with nymphs molting to adults especially to females. There appears to be two reproductive advantages to this feeding strategy. The first is that larger females can lay more eggs (Hafez et al., 1972). Also a shorter period of development provides a greater probability that a host will be available when reproduction can occur since both major hosts frequently switch burrows (Connat et al., 1986). Epidemiologically this behavior is important since disease transmission could occur either mechanically or via regurgitation thus circumventing the difficulties associated with transtadial and transovarial survival. Also, as the tick has such a diversity of hosts it makes an ideal reservoir for many diseases especially those that can infect a wide variety of species. Since ASF virus can survive a 60 day exposure to the external environment (Hess, personal communication), mechanical transmission by this method might occur.

The preference of Ornithodoros (P.) turicata americanus for any particular host is difficult to access. Gopher tortoises and gopher frogs are the most commonly parasitized hosts and in those cases where both coexist in the same burrow, comparison of blood meal identification shows a preference for gopher frogs with a ratio of 100 to

53 host feedings. If you delete those ticks that fed on both hosts, the ratio was 76 to 29 for frogs and tortoises, respectively. Preference differences between stages may not be comparable because of the low numbers obtained, population structural variability within and between burrows and unknown dispersion, both in time and space, of hosts and ticks in the burrows. However, the numbers obtained for each fed stage collected in those two host burrows were as follows: larvae, 5,31,5; first nymph, 18,12,1; second nymph, 3,6,3; third nymph, 1,18,6; late nymph, 1,9,8 ; female, 0,0,0 and male, 1,0,1; for tortoise fed, frog fed and tortoise and frog fed, respectively. These results show no strong trend, but the larval numbers for frog blood meals are especially high. Larvae of this species, like most tick species, have a strong negative geotaxis. To a lesser extent this is true of early nymphs. Since frogs are found near the entrances and tortoises deep in the burrow, this non-host orientating behavior may influence host selection so the numbers may not indicate preference.

Another method of assessing host preference is the comparison of the percentage of ticks fed in a population sample when different hosts are available. Student's t-tests were run and the analyses are summarized in Table

4-4. In contrast to the pooled data indicating frog preference, this analysis shows that a significantly greater percentage of the population will be fed when a tortoise is available rather than a frog. When the tortoise and frog together serve as hosts the feeding percentage significantly improves over the percentage of each host individually. Despite the numerous differences between the two sites the percentage values for each host did not differ significantly and so the data could be pooled for comparison. One cautionary factor on the interpretation of these data is that although burrows with tortoises only in them had a higher percentage of fed ticks than those with frogs, tortoise inhabited burrows yielded fewer individuals than did the other host inhabited burrows and so the relative weight of each fed tick was higher. Secondly, there were many burrows in which tortoise activity and habitation was suspected but contained no fed ticks. However when there was evidence of frogs, their presence was also indicated by the fed ticks found.

Blood meal analysis of biting insects, especially mosquitoes, and some acari has been commonly used in entomology to identify animal hosts. The serological test most commonly used to identify the source of arthropod blood meals have been the precipitin test (Washino and Tempelis, 1983). This test requires little equipment, the

Table 4-4. Student's t-test comparisons of percentages of the Ornithodoros t. americanus populations fed in burrows in which either tortoise, frog or tortoise and frog served as host.

	Mean (SD)	vs	Mean (SD)	Significance
L-tortoise vs L-frog	27.39 (18.73)		16.05 (13.17)	0.90
L-tortoise vs L-both	27.39 (18.73)		33.61 (24.49)	NS*
L-frog vs L-both	16.05 (13.17)		33.61 (24.49)	0.975
R-tortoise vs R-frog	24.66 (16.29)		13.81 (5.69)	0.99
R-tortoise vs R-both	24.66 (16.29)		25.86 (14.94)	NS*
R-frog vs R-both	13.81 (5.69)		25.86 (14.94)	0.95
L-tortoise vs R-tortoise	27.39 (18.73)		24.66 (16.29)	NS*
L-frog vs R-frog	16.05 (13.17)		13.81 (5.69)	NS*
L-both vs R-both	33.61 (24.49)		25.86 (14.94)	NS*
C-tortoise vs C-frog	25.46 (17.08)		15.64 (12.19)	0.995
C-tortoise vs C-both	25.46 (17.08)		31.10 (21.51)	0.90
C-frog vs C-both	15.64 (12.19)		31.10 (21.51)	0.99

L - Lochloosa

R - Robert s ranch

C - combined

* - NS signifies a non significant at P $\leq$ 0.01.

reagents are easily prepared and its execution and interpretation are not difficult. The Oucertlony immunodiffusion test used in this study is a variety of this test. More sensitive tests have been developed: fluorescent antibody (FA), passive hemagglutination inhibition (PHI) and enzyme-linked immunosorbent assay (ELISA). These systems were not developed for this project because of the increased development time, the complexity, the expensive tools and reagents, and the lack of necessary expensive equipment.

Blood meal identification on ticks is usually unnecessary as most ticks are collected from the animal they fed upon. Host identification in most argasids, which are not commonly collected while feeding on their host, is rarely required since there is usually only one species available for feeding. In a few cases several host species are available in the tick nidus and in those situations blood meal analysis is useful. There are several other examples, besides this study, which used serological blood meal analysis for soft tick/host identification. In North America this method was used to identify that both A.(A.) cooleyi and O.(A.) concanensis fed on passerine birds and that the latter also feed on bats (Cook, 1972). In Kenya, porcupines were identified as the major host for O.(O.) moubata in burrows (Heisch, 1954b), O.(P.) graingeri in

caves (Heisch, 1954a) and Argas (O.) brumpti (Heisch, 1954c). Walton (1957) studied O. moubata in domestic situations and found it fed on the variety of animals present, including man, domestic livestock and birds.

Host Suitability for Population Growth

The suitability of gopher tortoises verses gopher frogs to serve as hosts is difficult to access, but comparisons of changing population numbers and developmental stage conversions in the burrow population samples may be indicative. This was done by comparing burrow collection numbers between two periods in which at least one period showed host feeding. Comparison was done by observing the difference in numbers of each stage and between subsequent stages between the sampling periods. The time period between samples (approximately 50-60 days) was adequate for stage conversion and egg hatch.

Comparisons of population changes for each stage and between successive developmental stages was tested using Student's t-test between all variations in host availability. These data were summarized in Tables 4-5 to 4-26. For each stage or stage conversion, two tables were constructed. One set includes those combinations in which one of the two sampling periods did not have a host(s)

present. The second set includes all possibilities in which both sampling periods had hosts present.

Tables 4-5 to 4-9, covering changes in the number of immature individuals within a life stage between two collection samples show some obvious trends. In those cases in which a host becomes available in the second period there is a general increase in the number of individuals in that stage. This was profoundly evident when the hosts are frogs (F) or tortoise and frog (TF). For larval and nymphal stages the increases were often significantly greater than the modest population gains obtained when tortoises were present. Similarly, when the hosts vacated the burrows the larval and nymphal numbers decreased with the tortoise fed burrows experiencing the least losses. Host leaving related losses showed inconsistent trends in significance so no host correlated mortality could be established. Since the highest gains in larval and nymphal populations were significantly correlated with the presence of frogs it can be concluded that they are a more suitable host for population growth.

Frogs, like tortoises, show a high degree of burrow fidelity. They will live in only one or two burrows in a year, rarely three, and may inhabit that burrow for three or more years (Franz 1986b, personal communication). So

Table 4-5. Student's t-test comparisons of differences between sequential population samples of *Ornithodoros t. americanus* larvae in which one sample did not have any fed ticks present.

Mean (n)	Host Sequence					
	Ø-F	Ø-T	Ø-TF	F-Ø	T-Ø	TF-Ø
Ø-F 1.63 (n=8)	---					
Ø-T -17.23 (n=13)	.95	---				
Ø-TF 87.80 (n=5)	NS	NS	---			
F-Ø -2.25 (n=8)	NS	NS	NS	---		
T-Ø 12.19 (n=31)	.95	.99	NS	NS	---	
TF-Ø -31.00 (n=8)	NS	NS	NS	NS	NS	---

Ø - no feeding
 F - gopher frog
 T - gopher tortoise
 TF - gopher tortoise and frog

Table 4-6. Student's t-test comparisons of differences between sequential population samples of *Ornithodoros t. americanus* first nymphs in which one sample did not have any fed ticks present.

Mean (n)	Host Sequence					
	Ø-F	Ø-T	Ø-TF	F-Ø	T-Ø	TF-Ø
Ø-F 10.87 (n=8)	---					
Ø-T 0.15 (n=13)	.90	---				
Ø-TF 34.20 (n=5)	NS	NS	---			
F-Ø -2.50 (n=8)	.90	.90	NS	---		
T-Ø -1.48 (n=31)	.90	.95	NS	NS	---	
TF-Ø -30.50 (n=8)	.95	.90	.90	.90	.90	---

Ø - no feeding
 F - gopher frog
 T - gopher tortoise
 TF - gopher tortoise and frog

Table 4-7. Student's t-test comparisons of differences between sequential population samples of Ornithodoros t. americanus second nymphs in which one sample did not have any fed ticks present.

Mean (n)	Host Sequence					
	Ø-F	Ø-T	Ø-TF	F-Ø	T-Ø	TF-Ø
Ø-F 1.88 (n=8)	---					
Ø-T -0.23 (n=13)	.90	---				
Ø-TF 6.60 (n=5)	NS	.95	---			
F-Ø -2.25 (n=8)	.95	NS	.95	---		
T-Ø -0.32 (n=31)	.90	NS	.95	NS	---	
TF-Ø -13.25 (n=8)	.90	.90	.95	NS	.90	---

Ø - no feeding

F - gopher frog

T - gopher tortoise

TF - gopher tortoise and frog

Table 4-8. Student's t-test comparisons of differences between sequential population samples of Ornithodoros t. americanus third nymphs in which one sample did not have any fed ticks present.

Mean (n)	Host Sequence					
	Ø-F	Ø-T	Ø-TF	F-Ø	T-Ø	TF-Ø
Ø-F 3.62 (n=8)	---					
Ø-T -0.69 (n=13)	.90	---				
Ø-TF 0.20 (n=5)	NS	NS	---			
F-Ø -14.12 (n=8)	NS	NS	NS	---		
T-Ø 0.64 (n=31)	NS	.95	NS	NS	---	
TF-Ø -3.12 (n=8)	.90	NS	NS	NS	NS	---

Ø - no feeding
 F - gopher frog
 T - gopher tortoise
 TF - gopher tortoise and frog

Table 4-9. Student's t-test comparisons of differences between sequential population samples of Ornithodoros t. americanus late nymphs in which one sample did not have any fed ticks present.

Mean (n)	Host Sequence					
	Ø-F	Ø-T	Ø-TF	F-Ø	T-Ø	TF-Ø
Ø-F 7.00 (n=8)	---					
Ø-T -0.07 (n=13)	.90	---				
Ø-TF Ø (n=5)	NS	NS	---			
F-Ø 0.75 (n=8)	NS	NS	NS	---		
T-Ø 0.03 (n=31)	.90	NS	NS	NS	---	
TF-Ø -1.75 (n=8)	.90	NS	NS	.95	.90	---

Ø - no feeding
 F - gopher frog
 T - gopher tortoise
 TF - gopher tortoise and frog

that not only are they suitable, but they can sustain a population of O. t. americanus for years.

From the increase in larval numbers it is apparent that adult ticks readily parasitize frogs and tortoises. The changes in adult tick numbers when hosts are available are drastically different however, than those seen in the larval and nymphal stages. In Table 4-10 the percentage mean values for Ø-F and Ø-T display a decrease in adult numbers that accompany the availability of hosts. Also, when the host leaves the adult population increases. However, when both host species were available the population increased and decreased when both hosts left. No single reason is available, either behavioral or mathematical, that can be used to account for this response. Several different factors probably were involved in these results, each of which could increase or decrease the population available for sampling. These include: adults burrowing deep in the sand (as in laboratory colonies) to digest their meals and lay eggs (population decrease), quiescent ticks are stimulated into activity if physically displaced (population increase) and only newly emerged or hungry ticks are readily found roaming on the substrate (population increase). Mortality and migration might also occur.

Table 4-10. Student's t-test comparisons of differences between sequential population samples of Ornithodoros t. americanus adults in which one sample did not have any fed ticks present.

Mean (n)	Host Sequence					
	Ø-F	Ø-T	Ø-TF	F-Ø	T-Ø	TF-Ø
Ø-F -0.37 (n=8)	---					
Ø-T -0.62 (n=13)	NS	---				
Ø-TF 2.80 (n=5)	NS	.90	---			
F-Ø 1.12 (n=8)	.90	.95	NS	---		
T-Ø 0.29 (n=31)	NS	NS	NS	NS	---	
TF-Ø -6.37 (n=8)	.90	.95	.975	.975	.95	---

Ø - no feeding
 F - gopher frog
 T - gopher tortoise
 TF - gopher tortoise and frog

The following hypothesized scenario could explain these results. When the host enters the burrow some adults feed and then retreat to digest their meal. Other ticks return to the burrow to feed when stimulated from their deep sand refuges. These stimuli could possibly be increased CO₂ concentration or substrate disturbance. These stimulation processes however would take some time. Lastly, there are those that re-feed and those that are newly molted. The time periods for these activities are roughly 3 to 4 weeks after the host enters the burrow.

In the Ø-F and Ø-T samples the lower feeding rate and lesser amount of activity would possibly tend to only stimulate those newly emerged or hungry ticks, not the quiescent ones, and so decrease the number of adults available for sampling by drawing off those in the burrow into the sand or retreat into refuges to digest their blood meal. Fed argasid ticks produce volatile and non-volatile aggregation pheromones which would arrest movement and congregate ticks (Leahy, 1979). These chemicals may be responsible for the increased availability of adults on the sand surface that can be sampled in addition to those that have molted from nymphs after the host leaves, as in F-Ø and T-Ø.

In the case where both host species were present (TF) and the highest rate of feeding occurs, the adult mean

increases by nearly three. It would appear that the quiescent ticks, not normally available for sampling, are stimulated to emerge from their refuges in this circumstance. When the two hosts leave the adult tick population drops significantly. Mortality does not seem to be the most likely cause. Since fed argasid ticks do not respond strongly to pheromonal stimuli (Leahy, 1979) it would appear that the sated adults retreated to their refuges.

In Tables 4-11 to 4-15 are the Student's t-test comparisons of stage to subsequent stage conversions for those situations in which one of the two sampling periods did not have any host feeding. For all conversions the resulting mean differences suggest that when a frog was a tick host, either singly or with a tortoise, the number that transformed to the next stage was significantly greater than if a tortoise alone was available. The means show that when tortoises served as hosts, tick quiescence or mortality of a stage was more common than metamorphosis.

Comparisons of changes in population numbers when both sampling periods had host feedings are listed in Tables 4-16 to 4-26. Analyses of variance tests were insignificant except for the late nymph to adult conversion and the adult to adult means (significant at $=0.025$). Most single pair combinations were also insignificant. In

Table 4-11. Student's t-test comparisons of differences between larval and first nymphal numbers in sequential population samples of Ornithodoros t. americanus in which one sample did not have any fed ticks present.

Mean (n)	Host Sequence					
	Ø-F	Ø-T	Ø-TF	F-Ø	T-Ø	TF-Ø
Ø-F 5.38 (n=8)	---					
Ø-T -19.85 (n=13)	.95	---				
Ø-TF 34.00 (n=5)	NS	.90	---			
F-Ø -13.13 (n=8)	.90	NS	.90	---		
T-Ø -2.35 (n=31)	NS	.95	NS	NS	---	
TF-Ø -62.88 (n=8)	NS	NS	.90	NS	NS	---

Ø - no feeding
 F - gopher frog
 T - gopher tortoise
 TF - gopher tortoise and frog

Table 4-12. Student's t-test comparisons of differences between first nymphal and second nymphal numbers in sequential population samples of Ornithodoros t. americanus in which one sample did not have any fed ticks present.

Mean (n)	Host Sequence					
	Ø-F	Ø-T	Ø-TF	F-Ø	T-Ø	TF-Ø
Ø-F 1.12 (n=8)	---					
Ø-T 0.07 (n=13)	NS	---				
Ø-TF 7.80 (n=5)	.95	.975	---			
F-Ø -5.63 (n=8)	.99	.997	.995	---		
T-Ø -2.06 (n=31)	.95	NS	.995	.90	---	
TF-Ø -28.75 (n=8)	.90	.90	.95	NS	.90	---

Ø - no feeding
 F - gopher frog
 T - gopher tortoise
 TF - gopher tortoise and frog

Table 4-13. Student's t-test comparisons of differences between second nymphal and third nymphal numbers in sequential population samples of Ornithodoros t. americanus in which one sample did not have any fed ticks present.

Mean (n)	Host Sequence					
	Ø-F	Ø-T	Ø-TF	F-Ø	T-Ø	TF-Ø
Ø-F 4.75 (n=8)	---					
Ø-T -1.54 (n=13)	.95	---				
Ø-TF Ø.4Ø (n=5)	NS	NS	---			
F-Ø -3.63 (n=8)	.95	NS	.9Ø	---		
T-Ø -1.58 (n=31)	.95	NS	.975	NS	---	
TF-Ø -14.13 (n=8)	.95	NS	.9Ø	NS	NS	---

Ø - no feeding

F - gopher frog

T - gopher tortoise

TF - gopher tortoise and frog

Table 4-14. Student's t-test comparisons of differences between third nymphal and late nymphal numbers in sequential population samples of *Ornithodoros t. americanus* in which one sample did not have any fed ticks present.

Mean (n)	Host Sequence					
	Ø-F	Ø-T	Ø-TF	F-Ø	T-Ø	TF-Ø
Ø-F 5.62 (n=8)	---					
Ø-T -0.15 (n=13)	NS	---				
Ø-TF -0.60 (n=5)	NS	NS	---			
F-Ø -0.62 (n=8)	NS	NS	NS	---		
T-Ø -0.32 (n=31)	NS	NS	NS	NS	---	
TF-Ø -6.12 (n=8)	.90	.90	NS	NS	.90	---

Ø - no feeding
 F - gopher frog
 T - gopher tortoise
 TF - gopher tortoise and frog

Table 4-15. Student's t-test comparisons of differences between late nymphal and adult numbers in sequential population samples of Ornithodoros t. americanus in which one sample did not have any fed ticks present.

Mean (n)	Host Sequence					
	Ø-F	Ø-T	Ø-TF	F-Ø	T-Ø	TF-Ø
Ø-F 2.25 (n=8)	---					
Ø-T Ø (n=13)	.95	---				
Ø-TF 3.80 (n=5)	NS	.90	---			
F-Ø Ø.87 (n=8)	NS	NS	NS	---		
T-Ø 1.19 (n=31)	NS	.90	NS	NS	---	
TF-Ø -1.00 (n=8)	.90	NS	.90	NS	.90	---

Ø - no feeding

F - gopher frog

T - gopher tortoise

TF - gopher tortoise and frog

Table 4-16. Student's t-test comparisons of differences between sequential population samples of Ornithodoros t. americanus larvae in which both samples had fed ticks.^a

Mean (n)	Host Sequence								
	F-F	T-T	TF-TF	F-T	F-TF	T-F	T-TF	TF-T	TF-F
F-F 0.33 (n=3)	---								
T-T 0.07 (n=13)	NS	---							
TF-TF 16.00 (n=4)	NS	NS	---						
F-T -3.20 (n=5)	NS	NS	NS	---					
F-TF -0.60 (n=5)	NS	NS	NS	NS	---				
T-F 42.00 (n=2)	.975	.9995	NS	.9995	.9995	---			
T-TF 1.00 (n=2)	NS	NS	NS	NS	NS	.995	---		
TF-T -4.67 (n=3)	NS	NS	NS	NS	NS	.995	NS	---	
TF-F -5.00 (n=2)	NS	NS	NS	NS	NS	.975	NS	NS	---

a - F - gopher frog, T - gopher tortoise, TF - gopher tortoise and frog.

Table 4-17. Student's t-test comparisons of differences between sequential population samples of *Ornithodoros t. americanus* first nymphs in which both samples had fed ticks.⁸

Mean (n)	Host Sequence							
	F-F	T-T	TF-TF	F-T	F-TF	T-F	T-TF	TF-T
F-F 5.00 (n=3)	---							
T-T -0.69 (n=13)	.90	---						
TF-TF 14.75 (n=4)	NS	NS	---					
F-T 0.60 (n=5)	NS	NS	NS	---				
F-TF 1.40 (n=5)	NS	NS	NS	NS	---			
T-F 25.50 (n=2)	NS	NS	NS	NS	NS	---		
T-TF 1.00 (n=2)	NS	NS	NS	NS	NS	NS	---	
TF-T -1.33 (n=3)	.90	NS	NS	NS	NS	NS	.90	---
TF-F -1.50 (n=2)	.90	NS	NS	NS	NS	NS	.90	NS

a - F - gopher frog, T - gopher tortoise, TF - gopher tortoise and frog.

Table 4-18. Student a t-test comparison of differences between sequential population samples of Ornithodoros t. americanus second nymphs in which both samples had fed ticks.^a

Mean (n)	Host Sequence								
	F-F	T-T	TF-TF	F-T	F-TF	T-F	T-TF	TF-T	TF-F
F-F 31.66 (n=3)	---								
T-T 1.23 (n=13)	NS	---							
TF-TF 23.50 (n=4)	NS	NS	---						
F-T -1.40 (n=5)	NS	NS	NS	---					
F-TF 2.40 (n=5)	NS	NS	NS	NS	---				
T-F 3.50 (n=2)	NS	NS	NS	NS	NS	---			
T-TF 0 (n=2)	NS	NS	NS	NS	NS	NS	---		
TF-T 1.33 (n=3)	NS	NS	NS	NS	NS	NS	NS	---	
TF-F -1.00 (n=2)	NS	.90	NS	NS	NS	NS	NS	.90	---

a - F - gopher frog, T - gopher tortoise, TF - gopher tortoise and frog.

Table 4-19. Student's t-test comparisons of differences between sequential population samples of *Ornithodoros t. americanus* third nymphs in which both samples had fed ticks.^a

Mean (n)	Host Sequence								
	F-F	T-T	TF-TF	F-T	F-TF	T-F	T-TF	TF-T	TF-F
F-F 6.33 (n=3)	---								
T-T 0.76 (n=13)	.995	---							
TF-TF 11.25 (n=4)	NS	.90	---						
F-T -3.40 (n=5)	.995	.95	.90	---					
F-TF 1.00 (n=5)	.975	NS	NS	.90	---				
T-F 8.00 (n=2)	NS	.90	NS	.95	NS	---			
T-TF 1.00 (n=2)	*	*	NS	*	NS	*	---		
TF-T 1.33 (n=3)	.90	NS	NS	.90	NS	NS	NS	---	
TF-F 4.00 (n=2)	*	*	NS	*	.90	*	*	NS	---

a - F - gopher frog, T - gopher tortoise, TF - gopher tortoise and frog.

* - Value was divided by zero which gave an irrational number.

Table 4-20. Student's t-test comparisons of differences between sequential population samples of *Ornithodoros t. americanus* late nymphs in which both samples had fed ticks.^a

Mean (n)	Host Sequence							
	F-F	T-T	TF-TF	F-T	F-TF	T-F	T-TF	TF-T
F-F -3.33 (n=3)	---							
T-T -1.54 (n=13)	NS	---						
TF-TF 4.50 (n=4)	NS	.90	---					
F-T 0.60 (n=5)	NS	NS	NS	---				
F-TF -1.20 (n=5)	NS	NS	NS	NS	---			
T-F 0 (n=2)	NS	NS	NS	NS	NS	---		
T-TF 0.50 (n=2)	NS	NS	NS	NS	NS	NS	---	
TF-T -0.66 (n=3)	NS	NS	.90	.90	NS	NS	.90	---
TF-F 1.00 (n=2)	NS	NS	NS	NS	NS	NS	NS	NS

^a - F - gopher frog, T - gopher tortoise, TF - gopher tortoise and frog.

Table 4-21. Student's t-test comparisons of differences between sequential population samples of Ornithodoros t. americanus adults in which both samples had fed ticks.^a

Mean (n)	Host Sequence								
	F-F	T-T	TF-TF	F-T	F-TF	T-F	T-TF	TF-T	TF-F
F-F 11.33 (n=3)	---								
T-T 0.23 (n=13)	NS	---							
TF-TF 9.75 (n=4)	NS	.975	---						
F-T 1.40 (n=5)	NS	NS	.95	---					
F-TF 0.40 (n=5)	NS	NS	.975	NS	---				
T-F -8.50 (n=2)	NS	NS	.95	.90	NS	---			
T-TF -3.00 (n=2)	NS	NS	.975	NS	NS	NS	---		
TF-T 0.66 (n=3)	NS	NS	.95	NS	NS	NS	NS	---	
TF-F -1.00 (n=2)	NS	NS	.90	NS	NS	NS	NS	NS	---

^a - F - gopher frog, T - gopher tortoise, TF - gopher tortoise and frog.

Table 4-22. Student's t-test comparisons of differences between larval and first nymphal numbers in sequential population samples of Ornithodoros t. americanus in which both samples had fed ticks.^a

Mean (n)	Host Sequence								
	F-F	T-T	TF-TF	F-T	F-TF	T-F	T-TF	TF-T	TF-F
F-F 11.00 (n=3)	---								
T-T -1.38 (n=13)	NS	---							
TF-TF -41.25 (n=4)	NS	NS	---						
F-T -3.80 (n=5)	NS	NS	NS	---					
F-TF -4.80 (n=5)	NS	NS	NS	NS	---				
T-F 21.00 (n=2)	NS	.9995	NS	.975	.99	---			
T-TF 1.00 (n=2)	NS	NS	NS	NS	.975	NS	---		
TF-T -4.00 (n=3)	NS	NS	NS	NS	.90	NS	NS	---	
TF-F -1.00 (n=2)	NS	NS	.90	NS	NS	NS	NS	NS	---

a - F - gopher frog, T - gopher tortoise, TF - gopher tortoise and frog.

Table 4-23. Student's t-test comparisons of differences between first and second nymphal numbers in sequential population samples of Ornithodoros t. americanus in which both samples had fed ticks.^a

Mean (n)	Host Sequence								
	F-F	T-T	TF-TF	F-T	F-TF	T-F	T-TF	TF-T	TF-F
F-F 11.66 (n=3)	---								
T-T -2.30 (n=13)	NS	---							
TF-TF 10.25 (n=4)	NS	NS	---						
F-T -3.60 (n=5)	NS	NS	NS	---					
F-TF 0.80 (n=5)	NS	NS	NS	NS	---				
T-F -25.00 (n=2)	NS	NS	NS	NS	NS	---			
T-TF 0.50 (n=2)	NS	.90	NS	NS	NS	NS	---		
TF-T 0.66 (n=3)	NS	NS	NS	NS	NS	NS	NS	---	
TF-F -2.00 (n=2)	NS	NS	NS	NS	NS	NS	NS	NS	---

a - F - gopher frog, T - gopher tortoise, TF - gopher tortoise and frog.

Table 4-24. Student's t-test comparisons of differences between second and third nymphal numbers in sequential population samples of Ornithodoros t. americanus in which both samples had fed ticks.^a

Mean (n)	Host Sequence							
	F-F	T-T	TF-TF	F-T	F-TF	T-F	T-TF	TF-T
F-F 12.33 (n=3)	---							
T-T 0.07 (n=13)	.975	---						
TF-TF 12.00 (n=4)	NS	.90	---					
F-T -2.60 (n=5)	.95	NS	.90	---				
F-TF 1.60 (n=5)	.90	NS	NS	NS	---			
T-F -4.50 (n=2)	NS	NS	NS	NS	NS	---		
T-TF 1.00 (n=2)	*	*	NS	*	NS	NS	---	
TF-T 0 (n=3)	.95	NS	.90	NS	NS	NS	.90	---
TF-F 2.50 (n=2)	.90	.99	NS	.90	NS	NS	.95	.975

a - F - gopher frog, T - gopher tortoise, TF - gopher tortoise and frog.

* - Value was divided by zero which gave an irrational number.

Table 4-25. Student's t-test comparisons of differences between third and late nymphal numbers in sequential population samples of Ornithodoros t. americanus in which both samples had fed ticks.^a

Mean (n)	Host Sequence								
	F-F	T-T	TF-TF	F-T	F-TF	T-F	T-TF	TF-T	TF-F
F-F 3.33 (n=3)	---								
T-T -0.38 (n=13)	NS	---							
TF-TF 3.50 (n=4)	NS	NS	---						
F-T -2.60 (n=5)	.95	NS	.90	---					
F-TF 1.00 (n=5)	NS	NS	NS	NS	---				
T-F 3.00 (n=2)	NS	.9995	NS	*	NS	---			
T-TF 0 (n=2)	NS	NS	NS	.90	NS	.95	---		
TF-T 0.66 (n=3)	NS	NS	NS	.90	NS	.90	NS	---	
TF-F 1.50 (n=2)	NS	.95	NS	.95	NS	NS	NS	NS	---

a - F - gopher frog, T - gopher tortoise, TF - gopher tortoise and frog.

* - Value was divided by zero which gave an irrational number.

Table 4-26. Student's t-test comparisons of differences between late to adult numbers in sequential population samples of Ornithodoros t. americanus in which both samples had fed ticks.^a

Mean (n)	Host Sequence							
	F-F	T-T	TF-TF	F-T	F-TF	T-F	T-TF	TF-T
F-F -3.00 (n=3)	---							
T-T 1.23 (n=13)	.95	---						
TF-TF 12.25 (n=4)	.95	.95	---					
F-T 1.20 (n=5)	.90	NS	.90	---				
F-TF 0.20 (n=5)	NS	NS	.90	NS	---			
T-F -3.50 (n=2)	NS	NS	.95	NS	NS	---		
T-TF 0 (n=2)	*	*	.90	*	NS	*	---	
TF-T 1.33 (n=3)	NS	NS	.90	NS	NS	NS	NS	---
TF-F 2.00 (n=2)	.90	NS	.90	NS	NS	NS	.90	NS

^a - F - gopher frog, T - gopher tortoise, TF - gopher tortoise and frog.

* - Value was divided by zero which gave an irrational number.

some cases significant t-test values were generated but no trends were evident. There was no statistical demonstration that any pairs were preferred, except for TF-TF for late nymph to adult and adult to adult conversions. There were relatively greater numbers of positive mean values when a frog was in the second sampling period rather than a tortoise alone. This data supports the demonstration that although both hosts can serve as a means for population growth and do so when combined, frogs as hosts can generate a greater population increase in the tick population than tortoises.

Seasonality in Feeding and Population Growth

The tick, Ornithodoros t. americanus, fed on available hosts year round. Tables 4-27 and 4-28 show the numbers of burrows in which feedings occurred at the Lochloosa and the Robert's ranch sites, respectively. Figures 4-3 and 4-4 show the same data but as percentages of the burrows sampled. These tables illustrate several important points. First, the Lochloosa site had feeding occurring in approximately 40% of its burrows over the course of the experiment compared to less than 25% for Robert's ranch. Second, feeding occurs year round on both major hosts. Lastly, there exist trends in the frequency of parasitism for both major hosts, such that tortoises were more

Table 4-27. Seasonal feeding behavior of *Ornithodoros t. americanus* on hosts that inhabited gopher tortoise burrows at the Lochloosa site during 1984 and 1985.

Collection Period	Date	# of burrows with tortoise feeding	# of burrows with frog feeding	# of burrows with snake or unknown
orange	19 VI-25 VI	2	6	0
yellow	29 VII-20 VIII	2	5	0
red	26 IX-3 X	2	5	0
blue	14 XI-21 XI	4	4	0
green	2 I-8 I	4	2	1
mix 1	7 III-13 III	3	0	0
mix 2	25 IV-2 V	2	4	0
mix 3	6 VI-13 VI	5	3	3
mix 4	25 VII-1 VIII	0	1	1
last	27 IX-30 IX	1	0	1

Table 4-28. Seasonal feeding behavior of *Ornithodoros l. smericanus* on hosts that inhabited gopher tortoise burrows at the Robert's ranch site during 1984 and 1985.

Collection Period	Date	# of burrows with tortoise feeding	# of burrows with frog feeding	# of burrows with snake or unknown
orange	3 VII-29 VII	14	3	0
yellow	22 VII-18 IX	3	1	4
red	7 X-31 X	1	0	3
blue	5 XII-19 XII	2	1	0
green	17 I-8 II	2	1	0
mix 1	26 III-11 IV	4	0	1
mix 2	9 V-22 V	4	1	1
mix 3	20 VI-10 VIII	5	1	1
mix 4	20 VIII-9 IX	7	2	0
last	18 X-15 XI	3	1	2

Figure 4-3. Seasonal feeding behavior of Ornithodoros t. americanus on hosts that inhabited gopher tortoise burrows, expressed as percentages of total burrows that had feeding occurring during the 1984-1985 sampling periods at the Lochloosa pine flatwoods site.

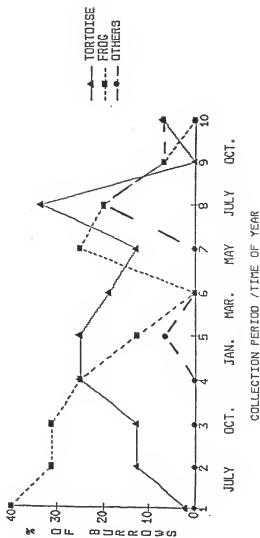
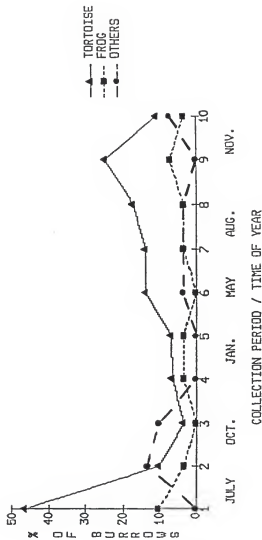


Figure 4-4. Seasonal feeding behavior of Ornithodoros t. americanus on hosts that inhabited gopher tortoise burrows, expressed as percentages of total burrows that had feeding occurring during the 1984-1985 sampling periods at the Robert's ranch sandhill site.



commonly parasitized in the cooler seasons and frogs in the warmer seasons. The last point on seasonality in host parasitism relates to host availability. Adult gopher frogs leave the burrows in winter, moving to breeding ponds, and return in April (Franz, 1986b). Also, in the cooler months gopher tortoises become less active and either do not leave their burrows or only make short feeding forays (Diemer, 1986).

Another trend that was observable seasonally was that in the cooler seasons the numbers in the tick population that were sampled decreases when compared to the warmer seasons. Adeyeye (1982) found that individuals during the winter season concentrated in the deeper portions of the burrows. Since sampling intensity was lower at deeper locations these lower values would be explained. This depression continues through the spring dry period. Another factor that may have contributed to Adeyeye's (1982) winter movement of ticks in the burrow was that the gopher frogs, which frequent the entrance areas in warmer months, are not present, so the ticks congregate around the tortoise deep in the burrow. Therefore the movement may not be temperature related. Also, when these sample populations were depressed the percentage of the population that were fed was higher than normal. These data were the primary cause of the highly significant means of percentage

tortoise fed per burrow in Table 4-4. Table 4-29 shows the means of the number of ticks collected and the percentage fed of those collected, regardless of host, versus collection period. Analysis of variance could not demonstrate a statistically significant F-value for this seasonal variation.

Mortality

Both abiotic and biotic mortality factors were identified. The major extrinsic mortality factor was low percentage soil water and the resultant low relative humidity. Whenever the percentage soil water fell below 0.5% large numbers of dead late stage nymphs and adults would be collected. Earlier stages probably also experience this mortality however their carcasses were rarely detected. This may have been due to them being scavenged by ants or other invertebrates, or became undetectable by degrading quickly and/or lost all fluorescence. Dead individuals under these conditions often outnumbered live ticks. At the more xeric Robert's ranch sandhill site these conditions were more common than at the Lochloosa location. Percentage soil water in the burrows was always less than at the surface, ranging from almost 5% down to 0.00%, but was commonly in the 1% range. At both sites from March to June some burrows would have

Table 4-29. Variation in the number of *Ornithodoros t. americanus* collected from gopher tortoise burrows in which a percentage had fed on an identifiable host.

Sample period	Lochloosa		Robert's ranch	
	# collected	% fed	# collected	% fed
orange 19-25 VI 3-29 VII	41.3 $\pm$ 5.7	22.1 $\pm$ 15.1	23.1 $\pm$ 22.7	18.1 $\pm$ 10.5
yellow 29 VII-20 VIII 22 VIII-18 IX	14.0 $\pm$ 12.7	26.8 $\pm$ 19.1	26.3 $\pm$ 36.5	18.8 $\pm$ 15.2
red 26 IX-3 X 17-31 X	74.3 $\pm$ 62.0	27.7 $\pm$ 15.4	12.0	16.7
blue 14-21 XI 5-19 XII	66.3 $\pm$ 96.8	25.9 $\pm$ 30.3	7.5 $\pm$ 2.1	52.8 $\pm$ 43.2
green 2-8 I 17 I-8 II	36.5 $\pm$ 26.4	24.4 $\pm$ 16.0	11.7 $\pm$ 6.4	24.4 $\pm$ 11.4
mix 1 7-13 III 26 III-11 IV	12.7 $\pm$ 13.3	41.7 $\pm$ 33.3	5.3 $\pm$ 2.4	28.2 $\pm$ 15.7
mix 2 25 IV-2 V 9-22 V	81.0 $\pm$ 154.4	27.3 $\pm$ 24.4	6.5 $\pm$ 7.7	35.7 $\pm$ 21.5
mix 3 6-13 VI 20 VI-10 VII	204.0 $\pm$ 263.2	10.7 $\pm$ 5.4	12.0 $\pm$ 6.4	23.8 $\pm$ 17.1
mix 4 25 VIII-1 VIII 20 VIII-9 IX	11.0	9.1	12.0 $\pm$ 12.3	23.1 $\pm$ 13.7
last 27-30 IX 18 X-15 XI	5.0	20.0	7.7 $\pm$ 5.5	32.9 $\pm$ 15.4

the low soil water percentages that signaled tick mortality. At Robert's ranch in October and November these low water conditions would again occur and apparently cause mortality. The importance of high relative humidity on the survival and distribution of Ornithodoros ticks has been well documented (Adeyeye, 1982; Avivi et al., 1973; Balashov, 1968), however measurements of available water in the soil environment where the tick reside had not previously been examined.

Starvation and/or desiccation was the major cause of death for those larvae, first and second nymphs in burrows in which no host was available. Later stages appeared not to experience significant decreases in population numbers due to long periods of host absence. Over a 50% reduction in larval numbers could be seen between 50 and 100 days after the host left the burrow. The early nymphal stages experienced a more gradual decline. Means and standard deviations were calculated for the maximum survival time after a host had left the burrow of each of these three stages. Most of the data originated from Robert's ranch, as feedings were less frequent at that site. The mean larval maximum survival time was 193.5 days ($\pm$ 91.3). First and second nymphal stage survival time was 210.6 ($\pm$ 110.6) and 243.4 days ($\pm$ 106.9), respectively. Student's t-test comparisons showed that only the larval and second

nymphal means were significantly different at the 0.90 level.

Predation was rarely demonstrated. Both invertebrate and vertebrate commensals were found to prey upon O. t. americanus. On one occasion each, the insect larva of the antlion, Glenurus gratis, and the therevid, Arenagena n.sp., were found preying upon a third instar nymph and a female, respectively. The ticks were collected with holes punched in their sides corresponding to the mouthparts of the two larvae.

Gopher frogs could not be induced to feed on ticks. Gopher mice would not usually eat them either. The mice would pick a tick up and let it drop. Only when the ticks were engorged would the mice feed. Then they would puncture the body near the legs or mouthparts with their teeth and squeeze the tick body, lapping up the blood and tick fluid. The husk of the tick would then be tossed away by the mouse. Only on a rare occasion (2 of 20) could any tick remains be detected in fecal pellets of mice.

Migration

Migration between burrows was demonstrated in the study. A total of 17 marked Ornithodoros t. americanus were collected in burrows from which they had not been released. There were 4 from Robert's ranch which included one male,

one female, one third nymph and one late nymph. Collected from *Lochloosa* were 8 males, 4 females and one late nymph - all were unfed at the time of collection. Although migration was detected by this method no rate or distance traveled could be determined because the research was not designed to measure this population parameter. The reasons for this conclusion are as follows: (1) All burrows received all shades of fluorescent dusts, a migration design would require each burrow to have an individual shade, (2) marked migrating larvae and nymphs can feed and shed their fluorescent marking prior to capture and (3) detection was serendipitous because migration could only be recognized when a marked individual was collected in a burrow which had not had any released individuals of that stage marked with that shade of fluorescent dust. So the age classes that were most likely to be detected as migrating are those that are few in numbers and do not molt, ie. adults.

There are two modes by which *Ornithodoros t. americanus* could migrate. Either by active migration, by leaving a burrow and dispersing into the environment, or by phoretic or passive migration, ie. by attaching to a host and detaching at a new site. Although the first is plausible and there is some evidence to suggest it occurs, it does not appear to be a strategy that evolution would

favor. The second is probably the more common method of dispersal.

During the course of this research burrows were examined over 500 times at the two study sites and other locations. Only in eight cases were ticks detected outside of a burrow. In three of these cases, ticks were found in sand that had recently been cleared from the burrow by a tortoise. In four cases, ticks were found buried in the dry sand of the burrow apron of inactive burrows. In the last case, ticks at an inactive burrow were on the surface of the apron. One tick was found walking along a branch laying on the apron. This last case provides the evidence for active dispersal. Previous experience has shown that this tick species is extremely hesitant to walk on any surface not covered with sand (Butler et al., 1984b). This observation shows that they will climb across obstacles and substrates they do not prefer. Also, they will move on the surface during daylight but only when the relative humidity is high as was shown by Adeyeye (1982) previously. The previous days rain had stiffened the soil so the ticks could not burrow in the sand outside of the burrow and the relative humidity at ground level was 85% (ambient RH=65%).

Only a few ticks were collected outside of the burrows. The numbers range from one to seven ticks (mean = 2.4). The youngest collected outside of a burrow was a

second instar nymph. The most commonly discovered stages were late nymphs and males (11 of 16).

There were no attempts to collect ticks from litter adjacent to the burrow entrances at the study sites. At the Newberry site where Adeyeye (1982) did his study over 5 square meters of litter adjacent to burrows was collected, sifted and berlezed. No Ornithodoros t. americanus were found.

Tick behavior outside of a burrow was observed at each time ticks were released. Normally all stages would within 3 cm. of their release on the apron orientate downward and run into the burrow. This was not light related orientation, but positive geotropism as on flat aprons they were more likely to go astray. If ticks were placed on the crest of an apron, where two downward slopes were available, the downward movements of the ticks would not necessarily lead them toward the entrance and many would move away from the burrow. Interestingly, this predilection for moving downhill would decrease the possibility of a migrating tick entering another burrow because approximately three quarters of the burrow circumference (apron area) is higher than the surrounding area. Humidity probably also plays a role in tick movement outside of a burrow. In humid conditions, movements were more hesitant and random. Perhaps the high relative

humidity interfered with their detection of the humidity gradient in the air near the burrow entrance. Humidity modified behavior was also demonstrated by Adeyeye (1982) who found that attraction of the tick out of the burrows during daylight by CO₂ release was most successful when the ambient relative humidity was in the 60-70% range.

In several burrows investigated, after they had become inactive, the ticks moved to within one meter of the entrance. Often within three months after this occurred the population would crash to the point where less than 10% of the original population numbers could still be sampled. The movement towards the burrow entrance was likely an effort to maximize the possibility of finding a host for a blood meal. Since the entrance area had more predators (eg. spiders) and lower humidity it also had a greater possibility for death. Similar distribution patterns were described for Ornithodoros tartakovskyi (Vasileva, 1976a, 1976b). The population could have succumbed to these pressures or during their host seeking behavioral movements at the burrow entrance or apron could have wandered out. However, no marked ticks from these holes were recognized in adjacent burrows even when the burrows were within three meters of each other.

Ornithodoros t. americanus are very sensitive to lowered humidity, especially at temperatures above 27°C.

The smaller the tick the less humidity stress necessary to kill it. Field collection techniques had to be developed to minimize this problem. It was found that as little as 10 minutes exposed to ambient air humidity on a 30-35°C summer day would kill most larvae. Even with the ticks' ability to burrow into the soil their chance of survival in migrating from one burrow to another seems slim. Avivi et al. (1973) drew similar conclusions for O. (P.) tholozani, stating that those individual ticks that ventured outside the caves at night were unlikely to survive for more than a few hours during the following day.

The major mode of migration from one burrow to another is proposed to be phoretic attachment to its primary hosts. As stated previously, O. t. americanus have been collected that remained attached to hosts captured away from their burrows. So it is likely that when the tortoise or frog or some other host leaves the burrow the ticks will go also. If the tortoise or frog after foraging go to another burrow and the ticks detach, migration would be accomplished.

Unfortunately none of the ticks that had migrated were recently fed so conclusive evidence for phoretic movement is unavailable. The fact that unfed migrant nymphs were collected tends to support active migration since feeding usually occurs rapidly once ticks attach, but these nymphs could just as easily have been dislodged as the host enters

another burrow prior to engorgement. This is especially likely if gopher tortoises were the host.

On four occasions, tortoises were captured and treated so as not to unduly stress the attached engorged ticks. The ticks were attached to the carapace and remained attached after capture for 3, 12-15, 22 and over 36 hours. This was similar to the infestations seen in California on desert tortoises (Ryckman and Kohls, 1962) although their infestations were heavier and may have been attached for longer time periods.

Three of the captured gopher frogs with attached ticks were held in the laboratory in Hotpack^R environmental chambers at 27°C and 95% RH. It was found that ticks remained attached longer to the frogs than tortoises. In one case three engorged ticks remained attached for at least 14 days. Perhaps the moist mucus and other liquids that bathed the frog and its tick parasites prevented tick desiccation, therefore allowing the ticks to remain attached longer.

Phoretic migration requires that the host must move from burrow to burrow. Both gopher tortoises and gopher frogs readily move in this manner. Franz (1986b) found that frogs normally use one or more burrows and similar evidence was seen at the Lochloosa study site. Gopher tortoises use several burrows as well. Diemer (1986)

found, using radiotelemetry at the Lochloosa site, that males used 4.3 burrows in a year, females used 2.3, sub-adults used 3 and juveniles used 1.6 burrows. This evidence supports the conclusion that Ornithodoros t. americanus uses its vertebrate hosts as modes of transport.

This phoretic attachment occurs not only with poikilotherms, but also with mammals. On October 17, 1986 Mrs. Debbie Akin collected an engorged female O. t. americanus from the belly area of her dog (Williston, Levy County). This tick subsequently produced over 100 viable eggs from this meal. There have been several unconfirmed reports of the tick attaching to the nose area of dogs also. Phoretic attachment of larvae and young nymphs to humans was also observed during this investigation. This is epidemiologically very important since Thomson (1985) concluded that phoretically attached O. (O.) moubata were the source of infection for primary ASF in rural Africa. A similar problem could occur in Florida with O. t. americanus especially considering the collection of this species on swine previously (Cooley and Kohls, 1944) and their presence in the burrows of the more motile burrowing owl (Milstre, 1986).

The ticks also utilize another method of "migration". In this case the migration is more temporal than physical. As inactive burrows are abandoned their entrances

accumulate debris and sand as the apron slides or flow in with the rain. Eventually the burrow closes and disappears. Ticks that remain in these closed burrows probably have near ideal conditions for survival, ie. moderate temperature and high humidity. If this Ornithodoros species is similar to those studied by Pavlovskii and Skrnnik (1968) some individuals might survive 20 years. All that is required is at some later date a tortoise excavates a new burrow that intersects the old one. Considering the large number of burrows used by a single tortoise (Diemer, 1986), the number of new burrows excavated in a colony each year, the persistence of tortoise colonies and the likelihood that a tortoise will select a location to dig a burrow for similar reasons as the original tortoise, it appears that burrow intersections are likely (Franz, personal communication). It also would be favorable for the gopher tortoise to dig a burrow that is likely to meet an older burrow since it could expend less energy and derive the same benefit, i.e. a new burrow.

This form of migration was demonstrated at the Lochloosa Wildlife Management Area. Hole 16N was abandoned and closed. Hole 114N was dug 2.5 meters away. Later 16N was reopened. Ticks marked in one hole were commonly extracted from the other. Using marked paper it was shown that 2.25 meters down hole 114N it intersected with 16N.

This temporal form of migration might explain the number of older staged ticks occasionally collected in new burrows.

Survivorship

The experimental design of this study was selected so as to utilize the Fisher-Ford method of population estimation (Fisher and Ford, 1947; Begon, 1979). Although not as informative as other mark/release/recapture methods, it is more accurate than the other methods when recapture rates are low (Bishop and Sheppard, 1973; Begon, 1979). Besides the basic assumption of a mark/release/recapture method it assumes that survivorship is constant (Begon, 1979).

Unfortunately, the recapture rates were so low that the calculated survivorship values were not consistently significant. When recaptures were higher, significant values were obtained. Whether survivorship is annually constant in the subterranean environment could not be answered by this study. Because of the low number of marked ticks recovered the Fisher-Ford estimates of survivorship for each stage, listed in Table 4-30, are underestimates. Also included in Table 4-30 are survivorship values calculated from the number of marked ticks released and the maximum length of time marked individuals survived in the field. Comparisons of these

Table 4-30. Longevity of *Ornithodoros t. americanus* under field conditions (observation period: 472-494 days).

Stage	Marked Individuals		Fisher-Ford Estimation	
	max. days survived	calculated survivorship	calculated survivorship mean (SD)	calculated days survived (1% of pop.)
larvae	208	.960	.740 (.255)	15
1st nymph	320	.976	.854 (.164)	29
2nd nymph	266	.973	.877 (.115)	35
3rd nymph	332	.980	.861 (.177)	30
late nymph	321	.979	.889 (.096)	39
female	272	.978	.893 (.113)	40
male	404	.983	.873 (.131)	33
length of life	2102 days 5.77 years			221 days 0.61 years

two sets of values indicate the inadequacy of the Fisher-Ford method for estimation of this population with the sampling system used. If accurate the Fisher-Ford survivorship values would suggest a life cycle length for field situations to be less than that obtained under optimum laboratory conditions (Beck et al., 1986).

The longevity of marked individuals was high. Larvae and first nymphs under laboratory conditions were not known to survive for the 208 and 320 days found in the field population. Considering the sensitivity to humidity of these stages they must move in the burrow frequently to maximize their exposure to favorable humidity conditions. The values for the later stages may not be maximum life spans since the experiment ran for less than 500 days and there is a moderately good chance that the life span lengths of these stages could be lengthened by further recaptures, especially females. In the laboratory individual males and females have been kept in near continuous egg production for two years with females producing as many as six egg batches. These data demonstrate that under field conditions the life span of Ornithodoros t. americanus may equal or surpass the long life spans of species in the genus reared under laboratory conditions seen in numerous citations and summarized by Pavlovskii and Skrynnik (1960).

Population Age Structure

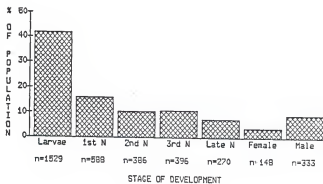
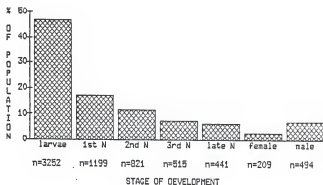
The age structure of the populations of Ornithodoros t. americanus sampled is shown in Figures 4-5 and 4-6. These figures show the dramatic effects of larval and first nymphal mortality on the age structure of the populations. The later stages appear to have a less severe mortality rate.

Seasonal changes also occurred in age structure with fewer early stages in the dry spring season at both sites but in the late summer these early stages became relatively more prevalent. This was associated with increased host feedings and increased soil humidity. This probably improved these early stages' survivorship. Also with the increased feeding more females molted from nymphs and increased female feeding was subsequently followed by improved reproductive output thus exponentially increasing larval numbers. See Table 4-29 for data on feeding, seasonality, and population increases.

The disparity in the sex ratio, 2.32:1, favoring males, does not reflect the genetic sex ratio of the species. Beck et al. (1986) and subsequent laboratory research has shown that the true sex ratio is close to 1:1 and females commonly undergo one or two more nymphal stages than males. These extra molts explain the unequal field sex ratio so the mortality rates effect the adult numbers

Figure 4-5. Age structure of the field population of Ornithodoros t. americanus in the sandhill habitat.

Figure 4-6. Age structure of the field population of Ornithodoros t. americanus in the pine flatwood habitat.



more than the opportunity for the extra nymphal feeding that females would require to equalize the ratio. This also means that the majority of late nymphs would molt into females. Another contributing factor to this disparity in the sex ratio is the mate-seeking behavior of the male. While looking for females, males are more commonly on the sand surface rather than buried and so are more likely to be sampled. Adeyeye (1982) also noted a male biased sex ratio in the field populations of this species.

Trends in Population Growth

The duration of host availability is an important factor in the maintenance or growth of Ornithodoros t. americanus populations. A measure of this is the number of sequential collection periods in which blood fed ticks can be collected. At Robert's ranch, the duration of host availability was usually short. In three burrows, host feeding was found in three sequential collection periods. On ten occasions host parasitism was found in two sequential periods. There were 30 burrow collections which had no subsequent host feeding during the following sample period.

At Lochloosa, host blood feedings over several sampling periods were more common. There were 12 positive burrow samples which were not followed by more feeding in

the next collection period. There were 13 situations in which sequential collection periods had host feeding. The number of sampling periods which had "continuous" feeding varied: seven for two periods, three for three periods and one each for four, six and seven collection periods.

The more common occurrence of hosts being available for long periods of time at Lochloosa was the primary reason for the higher tick populations in the burrows compared to those at Robert's ranch. This was due to several facts: (1) The longer a host is available the greater the possibility an individual tick will encounter it and feed, and (2) The longer a host is available for larval and early nymphal feeding, the probability of survival improves for ticks that can molt to those later stages that are more environmental durable and can survive long periods of starvation.

Unlike the cave populations of Ornithodoros (P.) tholozani that Avivi et al. (1973) studied, the populations of O.(P.) t. americanus never consisted entirely of late nymphs and females. In burrows with long histories of not being occupied (over 1 year), only larvae, first and second stage nymphs could not be collected, all other stages would be present.

When hosts become available and the ticks had an opportunity to feed the population grew and the age

structure changed. There were many cases in which the physical disturbance of a burrow showed that a tortoise or other vertebrate had visited a burrow, but apparently stayed for only a short period of time since no ticks feeding or changes in the population structure occurred. On several occasions, the visitation of a host could not be demonstrated by physical disturbance or the presence of fed ticks, because of the long time period between collection periods, but characteristic changes in the population structure indicated that host feeding had happened.

The sequence of changes in tick population structure after a vertebrate host was parasitized was moderated by several factors that were not consistently quantifiable. These factors include (1) the duration of host availability, (2) the period of time from the hosts' availability to the time of burrow sampling, (3) alteration of mortality factors and (4) the actual versus sampleable age and sex structure of the population. For these reasons, only trends in population growth could be established.

Only when frogs, tortoises or both served as hosts for O. t. americanus did population structure change. Snakes or unidentified hosts did not significantly affect the population as they were only responsible for one or two tick blood meals per burrow. Tick population growth in

gopher tortoise burrows usually followed a consistent pattern, barring misfortune. The first collection period in which host feeding was detected commonly exhibited the following changes: an increase in the number of ticks sampled, the appearance of low numbers of larvae and early nymphs, and a decrease in the number of females collected. These observations can be seen in Tables 4-5 through 4-15, which were discussed earlier. On the next sample period, regardless of host presence, tick larval numbers increased dramatically and usually an increase in the numbers of first and second nymphs occurred too. These large increases in larval numbers in the second period were due to successful female feeding and egg laying following the hosts' appearance. The nymphal increases are likely to be due to larvae that emerged from the eggs laid after the host appeared and/or from larvae and nymphs that were sequestered and subsequently moved to locations in the burrow that could be sampled.

The third sample period was accompanied by a decrease in larvae and to a lesser extent, early nymphs. It would appear that females do not undergo continuous production of progeny even when hosts are available. Late nymph and adult numbers usually increased, especially if a host was present. At later collection periods these adults would again produce offspring. In the few cases in which this

occurred hosts abandoned the burrows. Unfortunately, a casual relation between these high tick populations and burrow abandonment by both tortoises and frogs could not be proven, but was suspected.

Population Estimate

Fisher-Ford Estimate

Calculated population estimates using the Fisher-Ford method (Fisher and Ford, 1947) were consistently low. Calculated estimates were between 1 and 8 for each stage, 96% of the time. In 99% of the cases, the population estimate was less than the number of individuals collected.

Population estimates calculated using this method are dependant upon survivorship values. These survivorship values are calculated from recapture data (Table 4-38 for mean values). Bishop and Sheppard (1973) showed that in small populations both estimates and survivorship values were underestimated, especially at low sample intensities. Since survivorship values are calculated on a per day basis and the population estimation formulae progress at these daily intervals, the error was compounded significantly over the approximately 58 day period between the collection periods.

Other difficulties that may have also affected the performance of the calculation also existed. The

impossibility of multiple marking of ticks required that values derived from calculations on the probability of second recaptures be substituted for the actual numbers. Since recaptures were so low this correction factor was rarely used. Recapture evidence supports the hypothesis that a significant portion of the population was unsampleable and that these ticks used these refuges to avoid adversities present in the burrow. This use of refuges would decrease the calculated survivorship values and violate the "equal catchability" assumption.

Adeyeye (1982) used the less complicated Peterson estimate to generate estimated populations for O. t. americanus in gopher tortoise burrows. His more powerful vacuum may have sampled more of the refuges or his shortened sampling interval of two weeks was not enough time for the ticks to sequester themselves. His estimates however are of questionable accuracy since his sampling intensities were 10% or below which are accurate at levels below 0.5 (Robson and Regier, 1964; Roff, 1973). His estimates were probably accurate enough to provide a rough idea of population size (range = approximately 20-2000).

Removal Estimate

Using data obtained from three sequential samples taken from each burrow during a collection period the

invertebrate populations could be estimated. The maximum likelihood estimation method was used to calculate these estimates (Carle and Maughan, 1988; Carle and Strub, 1978). Tables 4-31 and 4-32 show the mean tick population estimates for the gopher tortoise burrows of Robert's ranch and Lochloosa, respectively. Table 4-33 shows the mean population estimates for each site during each collection period.

Pooling all ticks collected generally produced higher population estimates than the sum of each stages estimate, as predicted by Carle and Strub (1978). As the pooled catchability value dropped the disparity between these two estimates widened.

During sampling it was noted that the vacuum and hose sampled only one half to one third of the gopher tortoise burrow. As burrows became bigger, longer and more twisted the relative amount of the total available area sampled decreased. Since this removal estimation procedure is dependant upon area sampled, a correction factor of 2 or 3 should be applied to derived values to provide a more accurate estimate of the population size of Ornithodoros t. americanus. These values would then more closely resemble those of Adeyeye (1982). Figure 4-7 shows the mean estimated populations in burrows at both sites with the correction factors used. For Lochloosa the value used was

Table 4-31. Removal sampling population estimates of *Ornithodoros t. americanus* in gopher tortoise burrows sampled at the Robert S ranch sandhill site.

Burrow	Pooled Stage Estimate		Stage Estimate		Catchability	
	mean $\pm$ SD	(range)	mean $\pm$ SD	(range)	mean $\pm$ SD	(range)
7	18.5 $\pm$ 35.7	(0 - 119)	14.2 $\pm$ 25.0	(0 - 84)	0.38 $\pm$ 0.22	(0 - 0.7)
9	32.3 $\pm$ 60.9	(0 - 200)	29.8 $\pm$ 64.2	(0 - 211)	0.41 $\pm$ 0.25	(0 - 0.8)
10	12.0 $\pm$ 8.4	(1 - 28)	9.2 $\pm$ 5.5	(1 - 16)	0.56 $\pm$ 0.32	(0.2 - 1)
18	2.2 $\pm$ 1.5	(0 - 5)	2.3 $\pm$ 1.8	(0 - 6)	0.58 $\pm$ 0.33	(0 - 1)
22	37.8 $\pm$ 63.8	(2 - 215)	29.8 $\pm$ 56.1	(2 - 188)	0.37 $\pm$ 0.19	(0.2 - 0.7)
29	13.8 $\pm$ 17.1	(2 - 60)	11.6 $\pm$ 14.4	(2 - 51)	0.47 $\pm$ 0.21	(0.2 - 0.7)
43	6.4 $\pm$ 7.7	(0 - 21)	6.3 $\pm$ 7.5	(0 - 21)	0.46 $\pm$ 0.26	(0 - 0.6)
45	34.4 $\pm$ 24.4	(7 - 83)	23.8 $\pm$ 22.9	(7 - 83)	0.45 $\pm$ 0.20	(0.2 - 0.7)
50	10.8 $\pm$ 6.7	(2 - 24)	9.6 $\pm$ 6.0	(2 - 21)	0.49 $\pm$ 0.14	(0.3 - 0.7)
76	16.8 $\pm$ 19.3	(2 - 65)	13.9 $\pm$ 19.0	(2 - 65)	0.42 $\pm$ 0.20	(0.2 - 0.7)
80	32.1 $\pm$ 33.1	(3 - 93)	26.8 $\pm$ 28.1	(3 - 83)	0.39 $\pm$ 0.16	(0.2 - 0.6)
82	10.0 $\pm$ 5.9	(4 - 21)	8.3 $\pm$ 4.8	(4 - 20)	0.48 $\pm$ 0.17	(0.2 - 0.7)
103	20.1 $\pm$ 24.5	(4 - 84)	15.6 $\pm$ 19.5	(4 - 68)	0.36 $\pm$ 0.25	(0 - 0.8)
109	97.2 $\pm$ 158.8	(3 - 537)	63.3 $\pm$ 74.2	(3 - 251)	0.39 $\pm$ 0.19	(0.03 - 0.7)
110	131.6 $\pm$ 156.5	(2 - 434)	99.5 $\pm$ 123.9	(2 - 354)	0.33 $\pm$ 0.19	(0.08 - 0.6)

Table 4-31. (cont.)

141	8.5 ±	9.2 (0 - 31)	7.5 ±	7.6 (0 - 25)	0.51 ± 0.30 (0 - 1)
156	24.0 ±	22.1 (4 - 78)	20.9 ±	19.3 (4 - 67)	0.48 ± 0.20 (0.4 - 1)
157	12.1 ±	10.9 (0 - 31)	10.4 ±	9.5 (0 - 28)	0.41 ± 0.27 (0 - 1)
338	9.6 ±	11.0 (2 - 38)	7.6 ±	6.6 (2 - 21)	0.53 ± 0.24 (0.2 - 1)
341	12.1 ±	14.2 (1 - 49)	10.4 ±	11.6 (1 - 40)	0.49 ± 0.20 (0.3 - 1)
348	8.1 ±	6.6 (2 - 20)	7.7 ±	6.2 (2 - 20)	0.61 ± 0.15 (0.4 - 0.7)
355	1.9 ±	4.7 (0 - 15)	1.9 ±	4.7 (0 - 15)	0.38 ± 0.49 (0 - 1)
428	0.4 ±	0.7 (0 - 2)	0.4 ±	0.7 (0 - 2)	0.22 ± 0.36 (0 - 1)
439	1.6 ±	1.3 (0 - 4)	1.6 ±	1.3 (0 - 4)	0.43 ± 0.30 (0 - 1)
440	9.9 ±	10.7 (2 - 32)	8.3 ±	8.3 (2 - 26)	0.43 ± 0.16 (0.2 - 0.7)
447	32.2 ±	41.9 (1 - 130)	26.2 ±	37.5 (1 - 122)	0.46 ± 0.28 (0.2 - 1)
448	3.3 ±	3.5 (0 - 9)	3.3 ±	3.5 (0 - 9)	0.49 ± 0.31 (0 - 0.8)
451	4.7 ±	4.8 (0 - 11)	4.7 ±	4.9 (0 - 12)	0.41 ± 0.39 (0 - 0.6)
458	18.0 ±	20.3 (1 - 51)	12.9 ±	14.4 (1 - 38)	0.54 ± 0.32 (0.3 - 1)
472	8.7 ±	14.8 (0 - 50)	7.6 ±	12.1 (0 - 42)	0.49 ± 0.29 (0 - 1)

Table 4-32. Removal sampling population estimates of *Ornithodoros t. americanus* in gopher tortoise burrows sampled at the Lochloosa Flatwoods site.

Hole #	Pooled Stage Estimate mean + SD (range)	Stage Estimate mean + SD (range)	Catchability mean + SD (range)
8N	0.4 + 0.5 (0 - 1)	0.4 + 0.5 (0 - 1)	0.26 + 0.38 (0 - 1.00)
12N	385.0 + 425.8 (9 - 935)	392.0 + 563.7 (9 - 1660)	0.29 + 0.27 (0.01 - 0.75)
13N	69.8 + 100.4 (3 - 318)	47.7 + 63.2 (3 - 200)	0.37 + 0.23 (0.07 - 0.80)
16N	23.5 + 21.2 (1 - 60)	19.0 + 18.3 (1 - 57)	0.49 + 0.31 (0.16 - 1.00)
19N	84.7 + 89.5 (2 - 238)	65.0 + 68.8 (2 - 188)	0.34 + 0.27 (0.08 - 1.00)
20N	1.6 + 1.3 (0 - 4)	1.6 + 1.3 (0 - 4)	0.51 + 0.40 (0 - 1.00)
21N	28.0 + 25.9 (1 - 70)	14.5 + 11.9 (1 - 38)	0.44 + 0.35 (0.10 - 1.00)
27N	92.5 + 81.1 (13 - 243)	83.7 + 91.2 (11 - 272)	0.29 + 0.19 (0.10 - 0.75)
87N	169.0 + 220.1 (2 - 601)	172.1 + 231.2 (2 - 637)	0.57 + 0.27 (0.32 - 1.00)
114N	27.7 + 40.7 (0 - 132)	22.5 + 33.0 (0 - 108)	0.37 + 0.21 (0 - 0.75)
18S	205.9 + 249.9 (38 - 880)	147.4 + 172.3 (22 - 589)	0.20 + 0.10 (0.07 - 0.35)
21S	150.8 + 190.1 (5 - 598)	113.8 + 180.6 (5 - 591)	0.38 + 0.21 (0.07 - 0.63)
47S	93.5 + 137.5 (4 - 445)	61.1 + 80.1 (4 - 249)	0.33 + 0.24 (0.07 - 0.70)
62S	54.0 + 96.4 (0 - 319)	49.9 + 96.6 (0 - 320)	0.40 + 0.26 (0 - 0.67)
80S	111.4 + 247.4 (4 - 798)	106.5 + 245.5 (5 - 790)	0.37 + 0.16 (0.17 - 0.65)
82S	231.2 + 407.1 (2 - 1165)	207.4 + 369.8 (2 - 1061)	0.37 + 0.21 (0.11 - 0.65)

Table 4-33. Population variation in removal estimates of *Ornithodoros t. americanus* in gopher tortoise burrows at the Robert's ranch sandhill site and at the Lochloosa flatwoods site between collection periods.

Period	Robert's ranch		Lochloosa	
	PSE ^a	C ^b	PSE	C
Orange	41.5 + 102.2 (0 - 537)	0.44 ± 0.28	124.5 + 279.1 (0 - 880)	0.47 ± 0.34
Yellow	40.0 + 86.6 (0 - 434)	0.43 ± 0.20	59.3 + 79.6 (2 - 243)	0.45 ± 0.25
Red	27.5 + 67.8 (0 - 371)	0.46 ± 0.25	107.1 + 97.4 (0 - 318)	0.32 ± 0.25
Blue	21.4 + 33.5 (0 - 155)	0.37 ± 0.20	96.3 + 121.5 (0 - 403)	0.29 ± 0.17
Green	19.8 + 33.5 (0 - 182)	0.44 ± 0.26	180.0 + 266.3 (1 - 935)	0.46 ± 0.19

Table 4-33. (cont.)

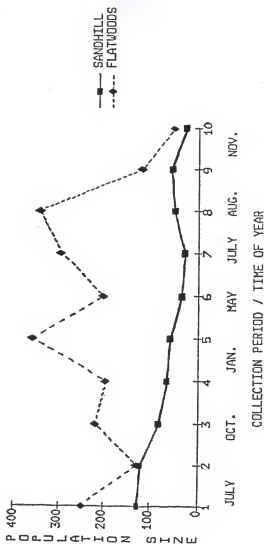
Mix 1	10.8 ± 12.7 (0 - 52)	0.40 ± 0.26	100.1 ± 213.4 (1 - 862)	0.39 ± 0.27
Mix 2	9.3 ± 12.3 (0 - 47)	0.49 ± 0.34	146.4 ± 343.5 (0 - 1165)	0.34 ± 0.25
Mix 3	16.6 ± 27.4 (0 - 130)	0.38 ± 0.22	171.2 ± 299.4 (0 - 842)	0.34 ± 0.30
Mix 4	18.9 ± 28.7 (0 - 119)	0.45 ± 0.29	58.9 ± 94.1 (0 - 319)	0.45 ± 0.29
Last	8.4 ± 15.6 (0 - 83)	0.58 ± 0.24	25.3 ± 36.1 (0 - 123)	0.56 ± 0.31

Nb. Numbers given in brackets are range values.

a - Pooled Stage Estimates.

b - Catchability

Figure 4-7. Mean estimated population size per gopher tortoise burrow for *Ornithodoros t. americanus* during the 1984-1985 sampling periods at both the Lochloosa flatwoods and the Robert's ranch sandhill sites. (Correction factors applied to removal sampling estimates (Carle and Maughan, 1980).)



2.0 since the burrows were shorter. For the Robert's ranch data 3.0 was used because of the longer burrows and increased depth of loose sand on the burrow floors that ticks could burrow in.

Biological Observations on Other Associated Invertebrates

Burrow Commensals

There are a large number of invertebrate commensals inhabiting the burrows of gopher tortoises. There have been three published studies on the burrow inguillines: Hubbard (1894, 1896), Young and Goff (1939), and the review paper by Woodruff (1982) that compiled all of the isolated taxonomic papers. Woodruff's (1982) paper included a checklist of invertebrates that had been reported in gopher tortoise burrows. During the present study a number of invertebrates were collected. Table 4-34 is a list of those species, their suspected association with the burrow (Milstrey, 1986) and the months in which they were collected. This list complements that of Woodruff's having many, but not all of the species listed, as well as many previously unreported species. Some of the species collected, that were identified by experts, were found to be undescribed new species.

Behavioral observations on a number of the species classified as commensals and opportunists were made during

Table 4-34. Invertebrates collected in gopher tortoise burrows at the Robert's ranch sandhill site and at the Lochloosa flatwoods site. Month of collection and its association with the burrow are also included.

Identity	Association	Sandhill	Flatwoods

Class Gastropoda			
Order			
Family Polygyridae			
<u>Praticolella bakeri</u> Vahatta	opportunistic	V-XII	IX

Family Zonitoidae			
<u>Glyphyalinia dalliana</u>			
(Pilsbry & Simpson)			
<u>Glyphyalinia indentata</u> (Say)	opportunistic	V-VI	-----
<u>Zonitoides arboreus</u> (Say)	opportunistic	-----	IX
<u>Hawesia minuscula</u> (Binney)	opportunistic	XII	III-XI

Class Arachnida			
Order Pseudoscorpionida			
Family Chernetidae			
<u>Chelanops affinis</u> Banks	commensal	I-XII	I-XII

Order Phalangida			
Family Phalangodidae			
<u>Crosbyella</u> sp.	commensal	I-XII	-----

Order Araneae			
Family Ctenizidae			
<u>Ummidia</u> sp.	opportunistic	-----	VI

Family Dictynidae			
<u>Dictyna</u> sp.	opportunistic	VI	V

Table 4-34. (cont.)

Family Gnaphosidae				
<u>Callilepis</u> sp.	opportunistic	-----		XI
<u>Zelotes limnophilus</u>				
Chamberlin				
<u>Gnaphosa sericata</u> (L. Koch)	opportunistic	IV		-----
sp. #1	opportunistic	V		-----
	opportunistic	-----		III
Family Clubionidae				
<u>Trachelas</u> sp.	opportunistic	-----		IV
<u>Scotinella</u> sp.	opportunistic	-----		VII
<u>Castianeira trilineata</u>				
(Hentz)				
<u>Castianeira gertschi</u> Kaston	opportunistic	XII		-----
<u>Phrurotimpus</u> ? sp.	opportunistic	V		-----
	opportunistic	II		-----
Family Anyphaenidae				
<u>Aysa</u> sp.	opportunistic	X		-----
Family Philodromidae				
<u>Philodromus</u> sp.	opportunistic	-----		I
Family Thomiscidae				
<u>Oxyptila</u> sp.	opportunistic	-----		III, IX
<u>Xysticus</u> sp.	opportunistic	V-VIII		-----
Family Salticidae				
<u>Habrocestum xerophilum</u>				
Richman				
<u>Thioclina</u> sp.	opportunistic	II-VIII		IX-XI
<u>Corythalia canose</u>	opportunistic	-----		XI, III
(Walckenaer)				
<u>Habrocestum bufoide</u>	opportunistic	-----		I-XI
<u>Habrocestum</u> Chamberlin & Ivie	opportunistic	-----		I-VIII
<u>Habrocestum</u> sp.	opportunistic	II-XI		-----

Table 4-34. (cont.)

<u>Habronattus n. sp.</u>	opportunistic	I	-----
<u>Habronattus sp.</u>	opportunistic	I-VIII	-----
Family Lycosidae			
<u>Pirata spiniger</u> Simon	opportunistic	VI-XII	VI-I
<u>Pirata sp.</u>	opportunistic	-----	IV-V
<u>Sosippus janus</u> Brady	opportunistic	-----	VIII
<u>Sosippus sp.</u>	opportunistic	V-VIII	VI-VIII
<u>Lycosa timuqua</u> Wallace	opportunistic	VIII	-----
<u>Lycosa carolinensis</u> Wallace	opportunistic	VIII	-----
<u>Lycosa sp.</u>	opportunistic	I-XII	I-XII
Family Agelenidae			
<u>Agelenopsis sp.</u>	opportunistic	-----	IX
Family Hahniidae			
<u>Neoantistea alachua</u> Gertsch	opportunistic	-----	III
<u>Neoantistea magna</u> (Keyserling)	opportunistic	III-IV	VI
<u>Neoantistea sp.</u>	opportunistic	I-II	-----
Family Theridiidae			
<u>Latrodectus mactans</u> (Fabricius)	opportunistic	VIII	VI
<u>Steatoda sp.</u>	opportunistic	-----	VI
<u>Argyrodes ? trigonum</u> (Hentz)	opportunistic	XII	-----
<u>Achaearanea porteri</u> (Banks)	opportunistic	VIII-IX	-----
Family Araneidae			
<u>Hypsosinga rubens</u> (Hentz)	opportunistic	I	-----
<u>sp. #1</u>	opportunistic	V	-----

Table 4-34. (cont.)

Family Linyphiidae			
<u>Florinda coccinea</u> (Hentz)	opportunistic	-----	III
<u>Ceratolops crenata</u> Emerton	opportunistic	-----	III
sp. #1 ?	opportunistic	-----	III-VII
<u>Ceratiolus cf. paludigera</u>			
Crosby & Bishop	opportunistic	XII-I	-----
<u>Lepthyphantes</u> sp.	opportunistic	II	-----
<u>Eperlingone</u> sp.	opportunistic	V	-----
Order Acari			
Suborder Mesostigmata			
Family Macrochelidae			
<u>Macrocheles dimidiatus</u> s. lat.	commensal	-----	IX
<u>Macrocheles</u> n. sp. #1	commensal	-----	VII
<u>Macrocheles</u> n. sp. #2	commensal	VII-IX	-----
<u>Macrocheles</u> n. sp. #3	commensal	VI	-----
Family Eviophididae			
<u>Alliphis</u> sp.	commensal ?	-----	X
Family Diplogyniidae			
<u>Brachysternum</u> sp.	commensal	I-IX	-----
Family Laelapidae			
<u>Haemolaelaps glaucowi</u> (Ewing)	commensal	I-XII	III
<u>Androlaelaps fahrenheitzi</u>	commensal	-----	I
(Berlese)	commensal	-----	IX
<u>Hypoaspis (Gaeolaelaps)</u> sp.	commensal	-----	
Family Macronyssidae			
<u>Ornithonyssus bacoti</u> (Hirst)	commensal	-----	IX

Table 4-34. (cont.)

Suborder Ixodida			
Family Argasidae			
<u>Ornithodoros turicata</u>	1-XII	commensal	1-XII
<u>americanus</u> (Marx)			
Family Ixodoidea			
<u>Ixodes scapularis</u> Say	IV	opportunistic	-----
<u>Amblyomma tuberculatum</u> Marx	1-XII	commensal	1-XII
<u>Amblyomma maculatum</u> Koch	-----	accidental	IX
Suborder Actiniedia			
Family Cheyletidae			
<u>Cheyletia bishoppi</u> Baker	VI	commensal	-----
Family Caeculidae			
<u>Microcaeculus</u> n.sp.	1-XII	accidental	-----
Family Trombididae			
sp. #1	V-X	accidental	-----
sp. #2	-----	accidental	III-IX
Family Trombiculidae			
<u>Eutrombicula cinnabaris</u>			
(Ewing)	-----	opportunistic	VI
<u>Parascia gurneyi</u> (Ewing)	VI-VIII	opportunistic	-----
<u>Walchia americana</u> (Ewing)	VI-VIII	opportunistic	-----
Suborder Acaridida			
Family Listerophoridae			
<u>Prolistophorus</u>			
<u>sparsilineatus</u> Fain	1-XII	commensal	V

Table 4-34. (cont.)

Suborder Oribatida			
Family Euphthiracridae			
<u>Rhysotritia ardua</u> (Koch)	opportunistic	I-XII	-----
Family Nothridae			
<u>Nothrus carolinae</u> Jacot	opportunistic	I-XII	I-XII
Family Liodidae			
<u>Liodes floridensis</u> Banks	opportunistic	I-XII	I-XII
Family Gymnodamaeidae			
<u>Alلودamaeus</u> sp.	opportunistic	I-XII	-----
Family Damaeidae			
<u>Lanibelba pini</u> Norton	opportunistic	I-XII	I-XII
Family Tectocephidae			
<u>Tectocephus</u> sp.	opportunistic	I-XII	-----
Family Oppiidae			
<u>Aeroppia floridana</u> (Banks)	opportunistic	I-XII	-----
Family Tregoribatidae			
<u>Eremgeozetes</u> sp.	opportunistic	I-XII	-----
Family Galumnidae			
<u>Pilogalumna</u> sp.n. <u>tenuiclava</u> (Bertese)	opportunistic	I-XII	-----
Family Oribatulidae			
<u>Schelorzibates</u> sp.	opportunistic	I-XII	-----
Family Chaunoproctidae			
<u>Xylobates</u> sp.	opportunistic	I-XII	I-XII

Table 4-34. (cont.)

Class Chilopoda			
Order Scolopendromorpha			
sp. #1	-----	opportunistic	III-VIII
Order Lithobiomorpha			
sp. #1	-----	opportunistic	III-VIII
Class Diplopoda			
Family Spirobolidae			
Chicobolus spingeri (Wood)			
Narceus sp.	XII	opportunistic	I-VI
	-----	opportunistic	VIII-XI
Family Castiopotidae			
Abacion sp.	I-XII	opportunistic	I-VIII
Class Insecta			
Order Collembola			
Family Sminthuridae			
several species	I-XII	opportunistic	I-XII
Order Orthoptera			
Family Gryllacrididae			
Ceuthophilus walkeri Hubbell	I-XII	commensal	I-XII
Family Tetrigidae			
sp. #1	IX-III	accidental	-----
Family Phasmatidae			
Anisomorpha bupestoides Stoll	-----	accidental	III
Family Blattellidae			
Parcoblatta sp.	I-XII	opportunistic	I-XII

Table 4-34. (cont.)

Order Heteroptera			
Family Reduviidae			
<u>Plofaria carolina</u> (Herrich-Schaeffer)	accidental	VII	-----
Family Cydnidae			
<u>Tominotus communis</u> (Uhler)	opportunistic	IV-IX	-----
Order Neuroptera			
Family Mymeleontidae			
<u>Myrmeleon carolinus</u> Banks	accidental	I-XII	I-XII
<u>Myrmeleon mobilis</u> Walker	accidental	-----	I-XII
<u>Glenurus gratus</u> (Say)	opportunistic	I-XII	-----
Order Coleoptera			
Family Carabidae			
sp. #1	accidental	-----	III-IV
sp. #2	accidental	IX, XII	-----
Family Staphylinidae			
<u>Bledius wudus</u> Herman	opportunistic	VII-X	-----
<u>Pinophilus confusus</u> Fall	accidental	-----	IX
<u>Megalopinus rufipes</u> (Le Conte)	accidental	XI	-----
<u>Astenus linearis</u> (Erichson)	accidental	-----	VI
<u>Neohyphus melanops</u> (Casey)	accidental	-----	III, XI
<u>Gabronthus mgogoricus</u> Tottenham	accidental	-----	VIII
<u>Philonthus</u> sp. near <u>gopheri</u> Hubbard	commensal	I-XII	I-XII
<u>Sepedophilus basalis</u> (Erichson)	opportunistic	II, X-XI	-----

Table 4-34. (cont.)

<u>Sepedophilus kitelevi</u> Campbell					
<u>Acrotona picescens</u> Notman	opportunistic		X	-----	
<u>Acrotona</u> sp.	accidental		VIII	-----	
<u>Atheta macrops</u> Notman	accidental		IX-XII	-----	
<u>Phanerota carinata</u> SeEVERS	accidental		VIII	-----	
or <u>fasciata</u> (Say)	accidental		I	-----	
<u>Thinobius</u> sp.					
Family Pselaphidae					
sp. #1	opportunistic		III-IX	-----	III-IX
Family Ptilliidae					
sp. #1	accidental		-----		VII
Family Leiodidae					
<u>Ptomophagus texana</u> Melander	commensal		I-XII	-----	
Family Scydmaenidae					
sp. #1	commensal		X	-----	
Family Scarabaeidae					
<u>Onthophagus polyphemus</u> Hubbard	commensal		I-XII	-----	I-XII
<u>Aphodius troglodytes</u> Hubbard	commensal		I-XII	-----	I-XII
<u>Ataenius cylindrus</u> Horn	opportunistic		-----		X-I
<u>Ataenius miami</u> Cartwright	opportunistic		IV-VII	-----	XI
<u>Ataenius ovatus</u> Horn	opportunistic		-----		III-XI
<u>Ataenius saramai</u> Cartwright	opportunistic		II-XII	-----	-----
<u>Ataenius simulator</u> Harold	opportunistic		-----		VI
Subfamily MeIoionthinae					
3 or 4 sp.	accidentals		XII-IV	-----	X-III

Table 4-34. (cont.)

Family Throscidae			
sp. #1	accidental	-----	I
sp. #2	accidental	VI	-----
Family Rhizophagidae			
sp. #1	accidental	IX	-----
Family Cucujidae			
sp. #1	accidental	-----	I-III
sp. #2	accidental	-----	VI
Family Ciliidae			
sp. #1	accidental	-----	VI
Family Histeridae			
<u>Chelyoxenus xerobatis</u> Hubbard			
sp. #2	commensal	I-XII	I-XII
sp. #3	opportunistic	I-XII	VIII-X
sp. #4	accidental	IX-II	VIII
sp. #5	accidental	XII	XI
sp. #6	accidental	VI	-----
	accidental	IX	-----
Family Plateridae			
<u>Platerini</u> sp.			
sp. #1	opportunistic	I-XII	I-XII
Conoderus sp.			
<u>Cardiophorinae</u>			
sp. #1	accidental	XII	VIII-IX
	accidental	VI	-----
Family Lathridiidae			
sp. #1	accidental	-----	III

Table 4-34. (cont.)

Family Alleculidae prob. <u>Mycetoclara</u> sp. (larva)	opportunistic	I-XII	I-XII
Family Tenebrionidae			
sp. #1	accidental	-----	VI
sp. #2	accidental	-----	VIII
sp. #3	accidental	X	-----
sp. #4	accidental	XII	-----
Family Phalacridae			
sp. #1	accidental	VIII-IX	-----
Family Crysmelidae			
Subfamily Cryptocephalinae			
<u>Cryptocephalus</u> sp. (larva)			
sp. #1	accidental	-----	III-VII
	accidental	III-VI	IV
Family Alticidae			
sp. #1	opportunistic	VIII	-----
Family Curculionidae			
sp. #1	accidental	-----	IV-V
sp. #2	accidental	VII-IX	-----
Family Tenebrionidae			
Blaptini			
sp. #1	opportunistic	II-XII	V-XII
sp. #2	opportunistic	V-XI	-----
Family Curculionidae			
sp. #1	accidental	V-XI	-----
sp. #2	accidental	XI-XII	-----

Table 4-34. (cont.)

Order Lepidoptera			
Family Limacodidae			
<u>Euclea delphinii</u> Bvd. (pupa)	accidental	-----	I
Family Acrolophidae			
<u>Acrolophus</u> n.sp. " <u>cheloniphilus</u> "	commensal	I-XII	?
<u>Acrolophus</u> sp.	opportunistic	-----	VI-XI
Family Noctuidae			
<u>Idia gopheri</u> (Smith)	commensal	I-XII	I-XII
Order Diptera			
Family Tipulidae			
<u>Nephrotoma</u> sp. (larvae)	opportunistic	-----	I-IV
Family Mycetophilidae			
<u>Phronia</u> sp.	opportunistic	-----	XI
<u>Rymosia</u> sp.	opportunistic	-----	I
Family Scleridae			
<u>Epidapus</u> sp.	opportunistic	III	-----
<u>Brachyneura</u> sp.	opportunistic	XII	-----
<u>Corynoptera</u> sp.	opportunistic	VII	-----
<u>Bradysia</u> sp. near	opportunistic	VI	VI-VII
<u>coprophila</u> Linter	opportunistic	VI	-----
<u>Bradysia</u> sp.			
Family Scatopsidae			
<u>Rhegmoclemia</u>	commensal	I-X	-----
(<u>Neorhegmoclemia</u>) n.sp.			

Table 4-34. (cont.)

Family Cecidomyiidae			
Subfamily Lesterminae			
new genus n.sp.			
<u>Arareta</u> sp.	II	-----	-----
			XIII
Subfamily Porricondylinae			
new genus n.sp.			
<u>Porricondyla</u> sp.	IX	-----	-----
<u>Claspettomylia</u> sp.	-----	-----	III
			V-IX
Subfamily Cecidomyilinae			
<u>Cecidomyiidi</u> 8 sp. (female)	III-VII		IV
<u>Schizomyia</u> sp.	-----		III
<u>Lobodiplosis</u> sp.	VII	-----	-----
<u>Kesseliella</u>			
sp. #1	X-II	-----	-----
sp. #2	XII	-----	-----
<u>Clinodiplosis</u>			
sp. #1	III-XI	-----	-----
sp. #2	XI	-----	-----
<u>Contarinia</u> sp.	-----		I-III
<u>Cecidomyia</u> sp.	-----		III
<u>Ledomyia</u> sp.	I-II	-----	-----
Family Therividae			
<u>Arenagena</u> n.sp.	I-XII	-----	-----
<u>Litolina tergisa</u> Say	IV	-----	-----
<u>Ozodiceromyia</u> notata			
(Wiedmann)	IV	-----	-----
<u>Ozodiceromyia</u> sp.	-----		III
<u>Cycloptelus pictipennis</u>			
(Wiedmann)	-----		VIII
opportunistic			
opportunistic			
opportunistic			
commensal ?			
accidental			
accidental			
accidental			
accidental			
accidental			
accidental			
accidental			
commensal			
opportunistic			
opportunistic			
opportunistic			
opportunistic			

Table 4-34. (cont.)

Family Asilidae <u>Asilus</u> n.sp.	commensal	V-IX	-----
Family Empididae <u>Drapetis</u> (<u>Drapetis</u>) sp. <u>Drapetis</u> (<u>Crossopalpus</u>) sp.	opportunistic commensal	I-XII	----- I-XII
Family Dolichopodidae <u>Condylostylus</u> sp. <u>Chrysotus</u> sp.	accidental	II	IX -----
Family Phoridae <u>Dohrniphora</u> sp. near <u>perplexa</u> (Brues) <u>Dohrniphora</u> <u>perplexa</u> (Brues) <u>Megaselia</u> <u>miniata</u> <u>Megaselia</u> sp. #2 sp. #3 sp. #4 <u>Apocephalus</u> <u>tenuipes</u> Borgmeier <u>Apocephalus</u> n.sp.	opportunistic opportunistic opportunistic opportunistic opportunistic accidental accidental	----- XII ----- I-XII I-XII VIII III-IV -----	XI ----- IX ----- I-XII I-XII ----- IV-V
Family Sphaeroceridae <u>Bitheca</u> <u>agarica</u> Marshall <u>Bromelocia</u> <u>winnemardi</u> Malloch <u>Pterogramma</u> sp. #1 sp. #2 <u>Coproica</u> n.sp. near <u>ferruginata</u> (Stenhammar)	opportunistic opportunistic opportunistic opportunistic commensal ?	VIII-IX VII-IX IX VIII VI-XII	----- ----- ----- ----- IV-XI
Family Milichiidae <u>Milichiella</u> n.sp. near <u>arcuata</u> (Loew)	commensal	VII-XII	-----

Table 4-34. (cont.)

Family <u>Drosophilidae</u> <u>Drosophila guttifera</u> Walker	opportunistic	-----	VI-VII
Family <u>Chloropidae</u> <u>Conioscinella triorbiculata</u> (Sabrosky)	opportunistic	VIII-X	-----
<u>Lachippelates pusio</u> (Loew)	opportunistic	IX	-----
<u>Tricimba melanchiolia</u> (Becker)	opportunistic	VIII-X	X
Family <u>Anthomyiidae</u> <u>Eutrichota gopheri</u> (Johnson)	commensal	I-XII	I-XII
Order <u>Siphonoptera</u> Family <u>Rhopalopsyllidae</u> <u>Polygenus floridanus</u> Johnson and Layne	commensal	I-XII	-----
Order <u>Hymenoptera</u> Family <u>Braconidae</u> <u>Alysiinae</u> sp. #1 sp. #2 <u>Microgastrinae</u> sp. #1 <u>Braconinae</u> sp. #1 sp. #2	commensal ? commensal ? accidental accidental accidental	VII IX ----- III-VII -----	----- ----- IX ----- III

Table 4-34. (cont.)

Family Pteromalidae			
sp. #1	accidental ?	I-III	-----
sp. #2	accidental ?	-----	VII
sp. #3	accidental ?	-----	I
sp. #4	accidental ?	-----	III
Family Eupelmidae			
sp. #1	opportunistic ?	-----	I
sp. #2	opportunistic ?	-----	IV-V
Family Encyrtidae			
sp. #1	accidental	V	-----
sp. #2	accidental	VIII	-----
sp. #3	accidental	-----	VI
sp. #4	accidental	-----	VI-VII
Family Eulophidae			
sp. #1	accidental	IV	-----
sp. #2	accidental	IX	-----
sp. #3	accidental	-----	I
sp. #4	accidental	-----	III
sp. #5	accidental	-----	IV
Family Eucolidae			
sp. #1	commensal ?	III-X	I
sp. #2	commensal ?	IX	-----
Family Diapriidae			
sp. #1	commensal ?	X	VI-IX
Family Scelionidae			
sp. #1	commensal ?	IX-III	-----
sp. #2	commensal ?	-----	IX-VI

Table 4-34. (cont.)

Family Platygastridae				
sp. #1	opportunistic	-----	I	-----
sp. #2	opportunistic	I-III	I-III	-----
sp. #3	opportunistic	-----	I-III	-----
sp. #4	opportunistic	-----	V-VII	-----
sp. #5	opportunistic	VI-VII	-----	-----
Family Bethyridae				
sp. #1	commensal	I-XII	-----	-----
Family Dryinidae				
sp. #1	accidental	-----	X	-----
Family Sphecidae				
sp. #1	accidental	-----	VI	-----
Family Formicidae				
Aphaenogaster fulva Roger	opportunistic	IV-XII	V-XI	-----
<u>Aphaenogaster carolinensis</u>				
Roger	opportunistic	-----	V	-----
Aphaenogaster ashmeadi Roger	opportunistic	-----	IX	-----
Conomyrma sp. #1	opportunistic	V	-----	-----
Conomyrma sp. #2	opportunistic	V-IX	III-V	-----
<u>Phaidole diversipilosa</u>				
Wheeler	opportunistic	-----	V	-----
Phaidole metallescens Emery	opportunistic	-----	IV	-----
Phaidole morrisi Ford	opportunistic	V	V	-----
Phaidole anastasi Emery	opportunistic	V	IX	-----
Phaidole adrianei Naves	opportunistic	-----	V	-----
<u>Hypoconera opacior</u> Ford	opportunistic	II-IX	V	-----
<u>Hypoconera punctatissima</u>				
(Roger)	opportunistic	-----	IX	-----
Prenolepis imparis (Say)	opportunistic	XII, II	I-VI	-----
<u>Proceratium pergandei</u> (Emery)	opportunistic	XII, VI	-----	-----

Table 4-34. (cont.)

<u>Strumigenys louisianae</u> Roger	opportunism	-----	V
<u>Pogonomyrmex badius</u>	opportunism	-----	-----
(Latreille)	opportunism	V	-----
<u>Solonopsis pergandei</u> Forel	opportunism	IV-IX	-----
<u>Solonopsis nickersoni</u> Thompson	opportunism	-----	IX
<u>Paratrechina parvula</u> (Mayr)	opportunism	V	-----
<u>Paratrechina faisonensis</u>	opportunism	-----	-----
(Ford)	opportunism	-----	IV
<u>Paratrechina arenivaga</u>	opportunism	-----	-----
(Wheeler)	opportunism	II-X	-----
<u>Camponotus castaneus</u>	opportunism	-----	-----
(Latreille)	opportunism	-----	IV
<u>Cyphomyrmex rimosus</u> (Forel)	opportunism	-----	VI
<u>Odontonachus brunneus</u>	opportunism	X	-----
<u>Crematogaster ashmeadi</u> Mayr	opportunism	V-VI	-----
<u>Forelius pruinosus</u> (Roger)	opportunism	IV	-----
<u>Formica pallidefulva</u> Mayr	opportunism	III-V	-----

the study. For many of the species collected, that were classified as opportunists or accidentals, little information other than the collection date is available. Presentation of observations on those species for which data exists were grouped according to their ecological role. Tables 4-35 and 4-36 show changes in the number of species present in the burrows annually at both sites. Figure 4-8 shows the locations within the burrow where some invertebrate species are usually found.

Invertebrate parasites

There were a number of parasites collected, both from vertebrates and invertebrates. The invertebrate parasites were mostly Hymenoptera. Unfortunately, genus and species level identifications were not completed. In most cases only one or two specimens were collected when they emerged from the vacuumed debris and no host information was available. Several parasites of the phorids, Megaselia species, were identified. These included the Eucoilidae species and the Diapriidae. These parasites emerged from the pupal stage of the fly. The species of Scelionidae collected in the winter from Robert's ranch were found to parasitize the larval stage of the Scatopsid fly, Rhegmoclemia bisaccatum Cook. Many other species collected undoubtedly were parasites of burrow commensals but no

Table 4-35. Annual changes in the number of invertebrate species present in gopher tortoise burrows and the percentage soil water at the Robert s ranch sandhill location.

Month	% Soil Water	# Parasites	# Vertebrate Parasites	# Predators	# Dung Decomposers	# General Decomposers ^a
Jan	1.11 ± 0.48	4	4	19	8	8
April	0.90 ± 0.55	8	5	13	10	9
May	0.34 ± 0.36	6	4	18	9	10
July	0.77 ± 0.43	8	5	20	12	14
Aug-Sept	2.33 ± 1.22	6	5	23	16	13
Oct	2.45 ± 0.96	7	5	18	16	12
Dec	1.65 ± 0.72	2	4	14	9	13

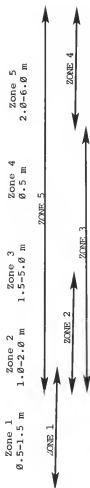
^a - macro

Table 4-36. Annual changes in the number of invertebrate species present in gopher tortoise burrows and the percentage soil water at the Lochloosa flatwoods location.

Month	% Soil Water	# Parasites	# Vertebrate Parasites	# Predators	# Dung Decomposers	# General Decomposers ^a
Jan	1.43 + 0.80	7	3	11	5	10
March	1.26 + 0.67	5	3	20	6	11
Apr-May	1.33 + 0.79	5	2	20	6	10
June	1.30 + 0.67	5	4	16	6	12
July-Aug	5.90 + 3.43	3	2	19	6	13
Sept	4.13 + 1.08	4	5	15	8	11
Nov	2.68 + 1.43	1	2	17	7	13

^a - ESACFO

Figure 4-8. Cross sectional diagram of a typical gopher tortoise burrow with the locations where some commensal invertebrates are found.



Zone 1: Myrmeleon
A. tuberculatum

Zone 2: Glenurus snails
Acrolophus Parcoblatta
Ataenius Asilus
Staphylinidae ants
Mycetophilidae Drosophila

Zone 3: Arenagena Lycosa
Aphodius other spiders
Ptomophagus Diplopoda
Onthophagus Cecidomyiidae

Zone 4: Onthophagus Sphaeroceridae
Chelanops Scatopsidae
Philonthus Drapetis
Crosbyella

Zone 5: Ornithodoros Eutrichota
A. tuberculatum Chelyoxenus
Ceuthophilus

definite proof exists since they emerged from burrow debris.

The vertebrate parasites identified were primarily acari. There were four tick species present in the gopher tortoise burrows, the previously discussed O. t. americanus and the gopher tortoise tick, Amblyomma tuberculatum. Large numbers of Amblyomma maculatum Koch larvae were encountered once. This is the most commonly encountered tick species parasitizing swine and other large animals (Greiner et al., 1984). The female apparently laid her eggs adjacent to or within the burrow. The Ixodes scapularis Say larva collected was attached to the head of a Peromyscus (P.) floridanus. This species will feed on a variety of lizards, birds and mammals. Ectoparasites on Peromyscus mice were also identified.

The gopher tortoise tick, Amblyomma tuberculatum Marx, is principally a parasite of the tortoise although it will parasitize other animals (Clements, 1956; Cooney and Hays, 1972). The life cycle and biology of the species were described in these papers and field studies on the tick were carried out by Clements (1956).

At both sites gopher tortoises were parasitized by this hard tick. At the Lochloosa site unattached ticks were not found. However, at the sandhill site tortoises were more heavily parasitized and free living stages were

present in the field. Free living unfed ticks were rarely encountered in burrows that were inhabited by a tortoise.

Unfed larvae at Robert's ranch were found both in the burrows and on the burrow apron. Of the larvae collected during burrow vacuuming, 958 were unfed and 40 were recently fed or in the process of molting. Unfed larvae were collected from September 5, 1984 through April 11, 1985, and from August 20 to the end of the study on November 15, 1985. Fed larvae were collected in the burrows from December 5, 1984 to April 11, 1985. The greatest number of larvae collected in a single burrow was 226. Maximal numbers per burrow (52.4 ± 36.9) occurred from late October to early November. The most fed larvae collected in a single burrow was 18 on January 17, 1985. Burrow samples in this January to February period accounted for 6 of the 12 burrow samples when fed A. tuberculatum larvae were collected. Blood meal analyses of 17 fed larvae showed 53% had fed on gopher tortoise and the remainder gave no reaction to alternative antisera tested.

Clements (1956) found in Alachua County that the peak of larval activity occurred in December compared to the earlier date of October and November obtained from the Putnam County site data. Also the period of larval activity was initiated one month earlier and was terminated one month later than Clements.

Unfed A. tuberculatum nymphs were present in burrows for more than half a year, April through November, 1985. In April: Mix 1 - 7 samples yielded 47 nymphs, May: Mix 2 - 25 samples yielded 131 nymphs, June and July: Mix 3 - 16 samples yielded 41 nymphs, August and September: Mix 4 - 5 samples yielded 10 nymphs and October and November: Last - 2 samples yielded 2 nymphs. No fed nymphs were ever collected. In comparison to Clements data, which was derived from nymphs on tortoises, the periods of peak abundance were similar. The Clements data showed no nymphs feeding past July, but the starved ticks in these data survived into late fall.

Adult unfed Amblyomma tuberculatum were collected year round. Peak numbers occurred from May to August. Between one and four unfed adults were collected in inactive burrows. Adults were found in approximately one quarter to one third of the burrows sampled. From October 1984 to April 1985 a few burrows yielded one or two adults. The sex ratio of males to females was 1.47 to 1 (75:51). Clements (1956) found males attached to tortoises year round, but females only from June to September. His data also showed a male bias in the sex ratio.

Although other hosts are known for this tick, the primary host for all stages is the gopher tortoise (Clements, 1956). The host seeking behavior of all stages

supports this conclusion. Unfed nymphs and adults were found in the mouth areas of inactive burrows. They were usually buried just beneath the dry sand. These stages were also found at the bases of clumps of vegetation adjacent to the burrow apron. When the burrow apron was disturbed the ticks would emerge from their hiding places and rapidly move into the burrow. Distances that ticks moved towards the burrow could be as great as 1.5 meters. Disturbances that initiated tick movements included soil movements, soil percussion (pounding the sand), CO₂ and the introduction of a tortoise. Alternative hosts, such as human flesh or gopher frogs, were treated as obstacles and ignored.

Unfed larvae early in the season would usually be found on the roof of the burrow, within 0.25 meters of the entrance. Later in the season some were found on the blades of wire grass, Aristida stricta, and occasionally other herbs. Larvae would be present at the tips of these blades from dusk until about 10am. During the heat of the day they were in the base of these grass clumps. Surprisingly, over 95% of larvae observed on the grass stems, were on stems that hung over or interfered with the access paths that tortoises used to move to and from the burrows. Plants or parts of plants that did not interface with the path did not have larvae present on them. Larvae

were rarely encountered in the environment at locations other than burrows. These host seeking behaviors are adapted to maximize the individual ticks' probability of encountering a gopher tortoise. This tortoise could be either the normal inhabitant or a brief visitor.

Mouse parasites identified include fleas, mites, ticks and lice. There were two species of mice examined, the Florida mouse, Peromyscus (Podomys) floridanus Chapman, and the cotton mouse, Peromyscus gossypinus (Le Conte). The fur mite, Prolistrophorus sparsilineatus Fain, were found on both species. One to three parasitic laelapids were also found per mouse. The Florida mice were infested with Haemolaelaps glasgowi (Ewing) and the cotton mice with Haemolaelaps sp., Androlaelaps fahrenheitzi (Berlese) and Ornithonyssus bacoti (Hirst). A louse, Hoplopleura hesperomydis (Osborn) was collected from a cotton mouse. Long term feeding ectoparasites on Florida mice include Ixodes scapularis Say and three chigger species. Also present on a Florida mouse was the mite predator Eucheyletia bishoppi Baker. Layne (1963) studied the internal and external parasites of the Florida mouse. The fur mite, the cheyletid, Ixodes scapularis and two of the three chiggers identified in this study are new host records.

The flea, Polygenus floridanus, was described by Johnson and Layne (1961) as a specific ectoparasite of the Florida mouse. They suggested that this isolation is due to a number of factors including the habitat specificity of the host, its unusual nesting structure, the lower number of fleas on hosts and the fact that they do not readily abandon their mouse hosts. Data collected on the over-all incidence of fleas and the mean number per infested host was similar to that reported by Johnson and Layne (1961) as approximately 33% and 2.3, respectively. Vacuum sample data indicated that flea populations in burrows could exceed 25 individuals, using the estimation procedure of Carle and Maughan (1980), but were usually around five. Tortoise burrows which were used as sites for a females' litter in the winter had the highest number of fleas extracted from them in the following seasons.

Invertebrate predators

The burrows had a wide variety of predators present. They included acari, spiders, pseudoscorpions, phalangids and insects. Predatory insects included ant-lions, hister beetles, dipterous larvae and adult Diptera.

The predacious acari identified were largely Macrocheles species. The specific prey was not identified but is believed to be the eggs and larvae of some of the

flies present, especially Eutrichota gopheri. Likewise, the prey of the pseudoscorpion, Chelanops affinis and the phalangid, Crosbyella sp. was not identified.

Several spider species in the genus Lycosa were found to utilize gopher tortoise burrows. There was usually only one individual per burrow and the same individual could be found in a burrow for several collection periods, indicating territoriality. The spider's burrows were usually found on the on the side of the incline from the burrow entrance to the apron. Most Lycosa during the warm periods of the day retreat into their burrows. The gopher tortoise burrow specimens did not do this, but were active all day long. Perhaps the high humidity, cooler temperatures and the prey availability kept the spiders active.

The larvae of the ant-lion, Glenurus gratis (Say), previous to this study were known only from tree holes (Miller and Stenge, 1983). Every tortoise burrow sampled at the Robert's ranch site had one or more specimens present. Eggs, the three larval stages and pupae were collected from the burrows. It appears that in most cases the life cycle was completed in one year. The coral pink eggs were laid in the burrows from June till September. In the summer all three larval instars were collected, but in winter and spring only the second and third instars were

present. Dozens of early stages were found but as the instars increased, numbers decreased dramatically. Cannibalism appeared to regulate larval numbers as parasites and predators could not be demonstrated. The Acrolophus n.sp. larva was the species primary food source.

There were two species of Drapetis, one at Lochloosa and one at Robert's ranch. The Robert's ranch species, Drapetis (Crossopalpus) sp., may be a commensal. This was indicated by its population size, behavior, the large number of larvae present and many adults emerged from collected burrow debris. This species was present only in burrows from which, Phoridae, Sphaeroceridae and/or Scatopsidae were collected. These may represent prey for this species. Adults were quite active in the burrows, especially in those that were inhabited. They would usually be seen working across the sand surface inside the burrow entrance. Most activities were done while walking and when flying they only flew a few centimeters, just above the sand floor. Adults were rarely collected as they consistently retreated deep into the burrow.

Thervid larvae were collected at both sites, but at the Putnam County site they were very common. These larvae were of an undescribed species in the genus Arenigena Irwin and Lyneborg. This species probably represents another example of an east to west species discontinuity induced by

Pleistocene habitat alterations, see Blair, (1958) and Howden (1963, 1966) for more examples. Larvae could only be reared on lepidoptera larvae in the laboratory. This suggests that it may feed on the Acrolophus normally in the field. It was always found in burrows that had this larva present also. Adults were rarely seen in the summer (May - August) when they emerged. Emerged females were very heavy and did not fly even when prodded. Females may mate and lay some eggs, in situ, so as to ensure that some larvae have a possibility of survival, which would lighten them and facilitate their departure.

An undescribed species of Asilus is currently being examined by Bullington and Beck (in prep.). This burrow commensal was present only at the Robert's ranch site from April to September and numbers peaked in June. The Anthomyiid fly, Eutrichota gopheri (Johnson), is the species' prey. Robber flies were seen only in burrows that appeared to be active or recently active with the Anthomyiid present. Only in 2 cases of 56 observations was more than one fly present in a burrow and in those exceptions they were a male and female. The robber flies were only found in burrows whose entrances were obvious and in direct sunlight.

The robber flies rest on roots or other projections that stick down from the roof of the burrow. They roost

within 10-30 cm. from the entrance during the day. It was difficult to get them to leave the burrow. When disturbed they will fly out of the burrow and land on adjacent vegetation or fly back in. When a tortoise enters a burrow they exit and land on the most central point of the carapace in relation to the sides of the burrow. It would then orientate upwards. Two strikes on Eutrichota were observed, once from the roof and once from the tortoise shell when it attacked after the Anthomyiid went around the tortoise.

Ants were observed as predators of the tick Ornithodoros t. americanus. On July 15, 1985, a released tick was attacked by several ant workers of Conomyrma sp.2. The workers succeeded in dragging the late nymph from the burrow entrance. The tick was rescued and the ants' attack had damaged one leg. This species and a Pheidole sp. were observed dragging tick carcasses.

Dung decomposers

There are supposed to be three commensal species of Scarabaeidae associated with gopher tortoise burrows, Copris gopheri Hubbell, Onthophagus polyphemi Hubbell and Aphodius troglodytes Hubbell. During this study over 15 locations in 4 counties were examined, and in no case was Copris gopheri recovered from the vacuumed material. This

large quantity of negative data leads me to suggest that the commensal role of this species be reevaluated. Besides these data, other collection data reported by Woodruff (1982) and the fact that this is the only species in the genus not associated with large animal dung (Woodruff, 1973) also suggest that a reevaluation is in order.

The remaining two species were very common and were present in the burrows year round, although the winter populations were often low. Observing trends and ratios in population numbers over a wide ecological cline, the following observations were made concerning these two species. In the very dry upland sandhills, the dung feeding and non ball-forming Aphodius troglodytes dominated the burrow scarab fauna. As the soil becomes more poorly drained the larger Onthophagus polyphemi becomes the dominant species. Those conditions that favor Onthophagus were seen in the flatwoods, near streams and swamps where burrows are shallow or when the soil contains quantities of clay.

In the discussion of Eutrichota gopheri (= Pegomyia gopheri) in Woodruff (1982) the coprophagous diet of its larvae was questioned. Vacuum collection however demonstrated that larvae of this species could only be obtained from fresh tortoise dung. Puparia of the fly were usually collected with an accumulated coat of cemented

sand. As many as 50 adults were found at one burrow, but 1 to 5 was common. Adults were rarely present in burrows that were inactive for long periods of time. Adult E. gopheri usually congregated within one meter of the entrance and rested on the roof of the burrow. The adult peak season was in early summer, prior to the emergence of the robber fly. If the robber fly was not present, relatively higher population levels were reached in July and August.

Several small dung breeding fly species were collected. Most species that were present were not commensals. These include those in the families: Phoridae, Chloropidae and Sphaeroceridae. The scatopsid, Rhegmoclema n.sp. is currently being classified as a commensal, but proof that this is the species' sole habitat is unavailable.

General decomposers

The Lepidoptera species, Idia gopheri (= Epizeuxis gopheri), has been reared successfully on gopher tortoise dung (Hubbard, 1894). Woodruff (1982) reserved judgement on whether I. gopheri was a true coprophage. Burrow collection at Robert's ranch and Lochloosa of both adults and larvae show that this year round available species does not require tortoise dung to complete its life cycle. In 7

of 22 instances, the burrows where this species was trapped had not been occupied for a period exceeding six months so the only available food source was the rapidly decomposing leaf litter that accumulates. Two adults were successfully reared from third instar larvae on a diet of leaf litter. So it can be concluded that this species is not a true coprophage.

Larvae, pupae and adults of the new species of Acrolophus were obtained, but eggs were not detected. Larval densities ranged up to 30 per burrow. In those repeatedly sampled burrows, population estimates, based upon removal sampling estimates (Carle and Maughan 1980), indicate larval numbers commonly are from 3 to 16. A few burrows that were not sampled routinely gave higher estimates, up to as high as 200. First instar larvae were found from May to November. All other stages were present year round. In the later part of the summer and early fall the pupating larvae probably were of two generations; the previous year's and offspring of the spring emergence. The life cycle is probably completed in one year (7 to 16 months).

Pupae and adults were infrequently collected in the burrows from May to September. Pupae were normally covered with sand and fecal pellets on the loose silk case. Apparently, pupation is triggered by unknown narrow

microclimatic conditions present in the burrow because when pupae were found there were commonly more than one and in other adjacent burrows none were found. Adults collected from burrows had wings that were badly tattered with few scales remaining on the body and wings. Flight in the enclosed space of the burrow and impact with the abrasive sand that covers the walls, roof and floor was probably responsible for the condition of the adults.

In the burrows as larval size increased, density decreased. Larvae were found to be cannibalistic in laboratory studies. The silk lined larval burrows were usually constructed just below the soil surface. Larval burrows could exceed 30 cm in length and were often branched. In the larval burrows, larvae traveled forward and backward in the trail, always facing the same direction. Feeding occurred at the entrance and fecal pellets were deposited on the soil surface at the other end.

Larvae were successfully reared on gopher tortoise fecal pellets. Tortoise fecal pellets are mostly partially digested wiregrass and some oak leaves. Although fecal material is available in the burrow, it's abundance is low and the competition for it is high. The amount of available fecal material is to low it support the Acrolophus population present. Also larvae are very common

in burrows that no longer have resident tortoises. In active burrows, tortoises frequently reexcavate their burrows and in those burrows larval number are significantly lower if not exterminated. Larval density was positively correlated with burrows that accumulate leaves and other debris. Apparently this rapidly decomposing organic leaf litter is their primary food source. Laboratory studies on limited numbers of larvae found that they would survive on the debris but that growth rates are lower.

The unique humidity situation in the burrow appears to be responsible for restricting the species to this habitat. In these sandhill gopher tortoise burrows relative humidities are in the mid to high 90's but the percent water in the soil is low (0 - 5%) year round. In the laboratory, larvae were found to be able to survive only within these limits. Pupating larvae leave their silk burrows and move to drier conditions where they then pupate. Pupae in the laboratory could be kept at room temperature and normal humidity levels.

The leaf litter present in the entrances attracts a number of general decomposers from the wider environment outside the burrow. These include the snails, millipedes, oribatid mites, gall midges (Lestremiinae) and soil inhabiting beetle larvae. This humid source of nutrients

also provides havens for fungi and so Drosophila sp.,
Phorids, Mycetophilidae and predatory Staphylinidae are
attracted.

CHAPTER V CONCLUSION

This field study on the invertebrates present in the burrows of the gopher tortoise concentrated on the ecology of Ornithodoros turicata americanus within the burrow to identify the parameters that maintain and promote growth of tick populations. Adeyeye (1982) examined some parameters of host seeking behavior of the tick outside the burrow. He showed that ticks will leave a burrow and feed on a pig thus demonstrating the potential for tick-pig ASF transmission. The immunological tools, currently being developed by Drs. Butler and Zam, are designed to identify the incidence of field exposure of swine to Ornithodoros ticks. This data in combination with Adeyeye's and my data will make it possible to establish a risk potential for tick transmission of African swine fever in Florida.

This field study found a wide variety of reptiles, amphibians and some mammals are potential hosts for tick populations within burrows. Several large animals such as deer, cattle and swine were present in the area. There was no evidence to suggest that these animals had a significant impact on the tick population within burrows. Whether these large animals were parasitized by Ornithodoros ticks was not tested.

Of the 18,581 O. t. americanus collected 6.3% were fed. Field data shows that gopher tortoises, gopher frogs, southern toads, opossums, snakes, dogs, man and probably the Florida mouse served as blood meal sources. The predominant hosts were the gopher tortoise and gopher frog. At the sandhill site the tortoise was the main blood source, but at Lochloosa, where tick populations per burrow were 3.5 times greater, the gopher frog was more commonly parasitized. Over 9.0% of all ticks that appeared fed gave no antisera reaction and so no host could be identified. The majority of these were ticks that had likely fed upon a common host but digestion had rendered their meal unidentifiable. A small percentage (1%), although recently fed, did not react with the test antigens and so had fed upon an unidentifiable host. These hosts could have been small burrow inhabitants, such as the southern toad or the lizards, or possibly large animals or birds that do not frequently encounter burrows.

Multiple host feeding was very common. Not only would all tick stages feed on all available hosts but between molts would feed more than once if a host were available. If these multiple fed ticks parasitize the same host or a host that was unidentifiable by the Oucuterlony test then multiple feeding would be unrecognized. This feeding method could increase disease transmission, especially

mechanical transmission, by increasing the number of hosts exposed. This method could also shorten the time necessary for a tick to reach adult stage, thereby improving survivorship.

The gopher frog was the preferred host of O. t. americanus, especially the larval stage. The frog was also a more suitable host for the growth of tick population compared to the tortoise. However, when both hosts were present, population growth was maximized.

There was no marked seasonality in feeding or population structure. Ornithodoros t. americanus fed year round on both major hosts, but tortoises were more commonly parasitized in the cooler months and frogs in the warmer months. This seasonality in host parasitism relates to host behavior and availability.

Mortality in O. t. americanus was primarily correlated with desiccation due to the low percentage of soil water in the burrow during the spring. No tick parasites were identified. Tick predators include Florida mice, ants, theriid and ant-lion larvae.

Migration of O. t. americanus from one gopher tortoise burrow to another was demonstrated. Phoretic dispersal on parasitized host is the proposed method for this movement, however active dispersal can not be disproved. A temporal form of migration was identified where ticks in a closed

burrow could enter a new burrow when that burrow's expansion intersected the remaining subterranean cavity of the old burrow. Epidemiologically this migration method is important because it could allow diseases to be maintained in an area, without transmission, possibly for twenty years or more.

The duration that marked individuals survived in the field was found to be quite high. Larvae were shown to live over 200 days in the field, a feat that could not be duplicated under laboratory conditions. This intimates that ticks move within the burrows so as to maximize their survivability. Calculations based upon the maximum time length survived by recaptured marked ticks indicate that a life cycle in the field could exceed six years. In burrows where hosts had not been present in over a year only larvae and early nymphs could not be sampled.

Hosts were rarely available for parasitism for extended periods of time so the long periods of time unfed ticks could survive was important in the maintenance of tick populations. Trends in field population growth reflected what would be expected from laboratory observations (Beck et al., 1986), except that females apparently fed and laid eggs when a host arrived and reproduction usually did not reoccur till several months later. This may have been evolutionarily selected, to

improve the females' chance of survival, and maximizing the reproductive potential since not all host incursions are of a long enough duration to support the early development of her offspring. No other hosts, identifiable or not, were demonstrated to alter population structure or initiate population growth other than gopher tortoises and gopher frogs.

The Fisher-Ford mark/release/recapture method (Fisher and Ford, 1947) was inadequate and inappropriate for estimating the population of O. t. americanus in gopher tortoise burrows. Removal estimation, using the method of Carle and Maughan (1980), generated estimates that were reasonable but observations from collection methods showed that those values should be multiplied by a factor of 2 or 3 since only one third to one half of the burrow surface was sampled. These corrected estimates show that sampleable populations may exceed 3000 individuals. These may still be underestimates since recapture data indicates that a significant portion of the population may be unsampleable, being sequestered in a refuge.

Eisenberg (1983) stated that the gopher tortoise is the keystone species in the sandhill environment. His comments were addressed specifically to the benefits that this species provides for the vertebrates present in the habitat. His statement is perhaps more pertinent for the

role that the burrow plays in the lives of the invertebrates of the sandhill and other environments where the tortoise lives. We are just beginning to learn of the role that this refuge plays in the surrounding habitats. The reason that this investigation was done was to provide an increase in our understanding of this significant ecological interface. The variation in the number of arthropods present at the two sites suggests that further investigation in intermediate habitats or geographically distant locations will be fruitful, not only in expanding our understanding of the role that these species play in the ecology of the burrow, but also new assemblages of species will be discovered that may provide more information on the evolutionary history and development of the gopher tortoise burrow community.

REFERENCES

Adeyeye, O.A. 1982. Field studies on Ornithodoros turicata (Duges) in the Gopher tortoise (Gopherus polyphemus Daudin) habitat in North Central Florida. Unpublished master's thesis. Univ. of Florida, Gainesville, Florida. 108pp.

Andrewes, C., H.G.Pereira and P.Wildy, (eds). 1978. Viruses of Vertebrates. 4th ed. Pailliere Tindall, London. 421 pp.

Auffenburg, W. 1969. Tortoise behavior and survival. Biol. Sci. Curric. Study. Patterns of Life Sci. Rand McNally and Co. Chicago, IL. 38pp.

Austin, F.J. 1978. Johnson Atoll virus (Quaranfil group) from Ornithodoros capensis (Ixodoidea: Argasidae) infesting a gannet colony in New Zealand. Amer. J. Trop. Med. Hyg. 27:1045-1048.

Avivi, A., M.Warburg and R.Galun. 1973. Ecological studies on the cave tick Ornithodoros tholozani and its distribution in Israel. Israel J. Entomol. 8:109-129.

Balashov, Y.S. 1968. Bloodsucking Ticks (Ixodoidea) - Vector of Diseases of Man and Animals. Nauka-Leningrad. 319 pp. (English translation: 1972. Misc. Publ. Entomol. Soc. Amer. Vol.8. No.5. 376 pp.)

Balashov, Y.S. 1972. Collecting the tick Ornithodoros papilles Bir. in caves with CO₂. Entomol. Rev. 51:122-123.

Beavers, P.C., T.C.Orihel and M.H.Johnson. 1974. Dipetalonema viteae in the experimentally infected jud, Meriones unguiculatus. II. Microfilaraemia in relation to worm burden. J. Parasitol. 60:310-315.

Beck, A.F., K.H.Holscher and J.F.Butler. 1986. Life cycle of Ornithodoros turicata americanus (Acari: Argasidae) in the laboratory. J. Med. Entomol. 23:313-319.

Bedford, G.A.H. 1931. Nuttalliella namaqua, a new genus and species of ticks. Parasitology 23:230-232.

Begon, M. 1979. Investigating animal abundance, capture-recapture for biologists. University Park Press, Baltimore, MD. 97 pp.

- Beldon, R.C., W.B. Frankenberger and D.H. Austin. 1985. A simulated harvest study of feral hogs in Florida. Study No. W-41-32XIII. Final Report. Florida Game and Freshwater Fish Commission Wildlife Research Laboratory, Gainesville, Florida. 82pp.
- Berge, T.O. 1975. International catalogue of Arboviruses including certain other viruses of vertebrates. 2nd Ed. Publ. No. CDC 75-8301 United States Dept. of Health, Education and Welfare, Public Health Service, Center for Disease Control, Atlanta, Georgia.
- Bhat, U.K.M. and M.K.Goverdhan. 1973. Transmission of Kyasanur forest disease by the soft tick Ornithodoros crossi. Acta Virol. (Prague) 17:337-342.
- Bishop, J.A. and P.M.Sheppard. 1973. An evaluation of two capture-recapture models using the technique of Computer Simulation. pages 235-252 in The mathematical theory of biological populations. M.S. Bartlett and R.W. Hiorens (eds.). Academic Press, London and New York.
- Bityukov, P.A. 1953. Experiments in transmission of theileriosis and anaplasmosis of sheep through Ornithodoros lahorensis and Haemaphysalis sulcata ticks. Trudy Inst. Zool. Akad. Nauk Kaz. SSR. 1:30-36. (English translation: NAMRU3 T3)
- Blair, W.F. 1958. Distributional patterns of vertebrates in the southern United States in relation to past and present environments. pages 433-468 in Zoogeography. Amer. Assoc. Adv. Sci., Washington, DC.
- Blanc, G. and J.Bruneau. 1955. Ornithodoros et coxiellose (Q Fever). Comp. Rend. Hebdo. Sea. Acad. Sci. 240:129-131. (cited in Hoogstraal 1985)
- Boardman, E.T. 1929. Ticks of the Gainesville area. Unpublished master's thesis. Univ. of Florida, Gainesville, Florida. 57pp.
- Brown, L.N. and G.C. Hickman. 1973. Tunnel system structure of the southeastern pocket gopher. Fla. Scientist 36:97-103.
- Bullington, S.W. and A.F. Beck. in prep. A new Asilidae from burrows of gopher tortoises.

Burgdorfer, W. 1956. The possible role of ticks as vectors of Leptospirae I. Transmission of Leptospira pomona by the argasid tick, Ornithodoros turicata and the persistence of this organism in its tissues. Exp. Parasitol. 5:571-579.

Burgdorfer, W. 1976. The epidemiology of the relapsing fevers. pages 191-200 in The Biology of Parasitic Spirochetes. R.C.Johnson, (ed.). Academic Press, New York.

Burgdorfer, W. 1980. Borrelia. pages 383-388 in Manual of Clinical Microbiology. E.H.Lennette, A.Balows, W.J.Hausler Jr. and J.P.Truant, (eds.). American Society of Microbiology, Washington, DC.

Burgdorfer, W. and C.R.Owen. 1956. Experimental studies on argasid ticks as possible vectors for tularemia. J. Inf. Dis. 98:67-74.

Butler, J.F., W.R.Hess, R.G.Endris and K.H.Holscher. 1984a. In vitro feeding of Ornithodoros ticks for rearing and assessment of disease transmission. pages 1075-1081 in Acarology VI Vol. 2. D.A.Griffin and C.E.Bowman, (eds.). Ellis Horwood Ltd., Chichester, England.

Butler, J.F., K.H.Holscher, O.Adeyeye and E.P.J.Gibbs. 1984b. Sampling techniques for burrow dwelling ticks in reference to potential African swine fever vectors. pages 1065-1074 in Acarology VI Vol.2. D.A.Griffiths and C.E.Bowman, (eds.). Ellis Horwood Ltd., Chichester, England.

Butler, J.F., D.D.Wilson, G.I.Garris, H.G.Koch, J.M.Crum and V.E.Castellanos. 1985. Survey for potential soft tick (Acari: Argasidae) vectors of African swine fever on the island of Hispaniola. Exp. Appl. Acarol. 1:63:72.

Buxton, P.A. and B.Weitz. 1953. The role of digestion of bloodmeals of various haematophagous arthropods as determined by the precipitin test. Bull. Entomol. Res. 44:445-450.

Carle, F.L. and O.E. Maughan. 1980. Accurate and efficient estimation of benthic populations: A comparison between removal estimation and conventional sampling techniques. Hydrobiologia 71:181-187.

Carle, F.L. and M.R. Strub. 1978. A new method of estimating population size from removal data. Biometrics 34:621-630.

Chastel, C., H. Pailly-Chouman and G. Le Lay-Fogues. 1981. Pouvoir pathogene naturel pour l'homme d'un variant antigenique du virus Soldado isle au Maroc. Bull. Soc. Path. Exot. 74:499-505 (cited in Hoogstraal 1985)

Chastel, C., F. Le Goff and G. Le Lay-Fogues. 1983. Antigenic variants of the Soldado virus (Nairovirus, Bunyaviridae) isolated in different parts of the world. Acta Virol. (Prague) 27:51-58.

Chastel, C., A.J.Main, C.Guiguen, G.LeLay, M.C.Quillien, J.Y.Monnat and J.C.Beaucourner. 1985. The isolation of Meaban virus, a new flavivirus from the sea bird tick Ornithodoros maritimus in France. Arch. Virol. 83:129-140.

Clements, B.W. Jr. 1956. The biology and life history of the gopher tortoise tick Amblyomma tuberculatum Marx. Unpublished master's thesis. Univ. of Florida, Gainesville, Florida. 85pp.

Clifford, C.M. 1979. Tick borne viruses of seabirds. pages 83-100 in Proceedings of the 2nd International Symposium, Artic Arboviruses. Mont Gabriel, Canada. May 1977. (cited in Hoogstraal 1985)

Clifford, C.M., H.Hoogstraal, J.F.Keirans, C.A.Rice and W.F.Dale. 1978. Observations on the subgenus Argas (Ixodoidea: Argasidae: Argas) 14. Identity and biological observations of Argas (A.) cucumerinus from Peruvian seaside cliffs and a summary of the status of the subgenus in the Neotropical faunal region. J. Med. Entomol. 15:57-73.

Clifford, C.M., H.Hoogstraal, F.J.Padovsky, D.Stiller and J.E.Keirans. 1980. Ornithodoros (Alectrobus) ambius (Acarina: Ixodoidea: Argasidae): identity, marine bird and human hosts, virus infections and distribution in Peru. J. Parasitol. 66:312-323.

Clifford, C.M., H.Hoogstraal, M.A.Poshdy, H.Y.Wassef, J.E.Keirans and M.D.Corwin. 1983. Observations on the subgenus Argas (Ixodoidea: Argasidae: Argas). 18. Haller's organ roof and anterior pit setae. J. Parasitol. 69:967-976. (Publ. in 1984)

Clifford, C.M., J.E.Keirans, H.Hoogstraal and D.Corwin. 1976. Observations on the subgenus Argas (Ixodoidea: Argasidae: Argas). A. (A.) dalei, new species parasitizing the burrowing owl in Peru. Ann. Entomol. Soc. Amer. 69:917-925.

Clifford, C.M., G.M.Kohls and D.E.Sonenshine. 1964. The systematics of the subfamily Ornithodorinae (Acarina: Argasidae). I. The genera and subgenera. Ann. Entomol. Soc. Amer. 57:429-437.

Condy, J.B., R.A.Norval, N.K.Blackburn and D.Clements. 1980. The effects of bites of Argas brumpti (Acarina: Argasidae) on humans. Cent. Afr. J. Med. 26:212-213.

Connat, J.L., J.Ducommun, P.A.Diehl and A.Aeschlimann. 1986. Some aspects of the control of the gonotrophic cycle in the tick Ornithodoros moubata (Ixodoidea, Argasidae). pages 194-216 in J.R.Saver and J.A.Hair (eds.). Morphology, Physiology and Behavioral Biology of Ticks. Ellis Horwood Limited, Chichester, England.

Cook, B. 1972. Hosts of Argas cooleyi and Ornithodoros concanensis (Acarina, Argasidae) in a cliff-face habitat. J. Med. Entomol. 9:315-317.

Cooley, R.A. and G.M.Kohls. 1944. The Argasidae of North America, Central America and Cuba. American Midland Naturalist. (Monograph) 1:1-152.

Cooney, J.C. and K.L. Hays. 1972. Bionomic of the gopher tortoise tick Amblyomma tuberculatum Marx. J. Med. Entomol. 9:239-245.

Crowle, A.S. and J.L.Cline. 1977. An improved strain for immunodiffusion tests. J. Immuno. Meth. 17:379-381.

Cunliffe, N. 1922. Some observations on the biology and structure of Ornithodoros savignyi Audouin. Parasitology 14:17-26.

Da Massa, A.J. and H.E.Alder. 1979. Avian spirochetosis: Natural transmission by Argas (Persicargas) sanchezi (Ixodoidea: Argasidae) and existence of different serological and immunological types of Borrelia anserina in the United States. Amer. J. Vet. Res. 40:154-157.

Darwish, M.A. and H.Hoogstraal. 1981. Arboviruses infecting humans and lower animals in Egypt. A review of thirty years of research. J. Egypt Publ. Health. Assoc. 56:1-112.

Darwish, M.A., H.Hoogstraal, T.J.Roberts, I.P.Ahmed and F.Omar. 1983. A seroepidemiological survey for certain arbovirus (Togaviridae) in Pakistan. Trans. Roy. Soc. Trop. Med. Hyg. 77:442-445.

Davis, G.E. 1939. Relapsing fever: Ornithodoros hermsi a vector in Colorado. Publ. Health Rpts. 54:2178-2180.

Davis, G.E. 1941a. Ornithodoros turicata: The Male: Feeding and copulation habits, fertility, span of life, and the transmission of relapsing fever spirochetes. Publ. Health Rpts. 56:1799-1802.

Davis, G.E. 1941b. Ornithodoros parkeri Cooley: Observations on the Biology of this tick. J. Parasitol. 27:425-433.

Davis, G.E. 1942a. Ornithodoros parkeri and relapsing fever spirochetes in southern Idaho. Publ. Health Rpts. 57:1501-1503.

Davis, G.E. 1942b. Species unity or plurality of the relapsing fever spirochetes. Science 18:41-47.

Davis, G.E. 1942c. Tick vectors and lifecycles of ticks. Amer. Assoc. Adv. Sci. Publ. 18:66-76.

Davis, G.E. 1943a. Experimental transmission of the spotted fevers of the United States, Columbia and Brazil by the argasid tick Ornithodoros parkeri. Publ. Health Rpts. 58:1201-1208.

Davis, G.E. 1943b. Relapsing fever: The tick Ornithodoros turicata as a spirochete reservoir. Publ. Health Rpts. 58:839-842.

Davis, G.E. 1943c. American Q Fever: Experimental transmission by argasid ticks Ornithodoros moubata and O. hermsi. Publ. Health Rpts. 58:984-987.

Davis, G.E. 1955. Observations on the biology of the argasid tick Ornithodoros puertoricensis Fox. J. Parasitol. 41:76-79.

Davis, G.E. and A.J. Mauros. 1956. Concerning the life cycle of Ornithodoros coniceps (Canestini) 1890 (Ixodoidea, Argasidae). J. Egypt Publ. Health. Assoc. 31:69-74.

Davis, G.E. and M.E. Walker. 1940. Ornithodoros hermsi: Feeding and molting habits in relation to the acquisition and transmission of relapsing fever spirochetes. Publ. Health Rpts. 55:492-504.

De La Cruz, J. 1976. Notas adicionales a la fauna de Garrapatas (Ixodoidea) de Cuba. V. Una nueva especie de genero Antricola Cooley y Kohls, 1942 (Argasidae). Poeyana 151:1-8.

De La Cruz, J. 1978a. Notas adicionales a la fauna de Garrapatas (Ixodoidea) de Cuba. VI. Cuatro nuevas especies del genero Antricola Cooley y Kohls, 1942 (Argasidae: Ornithodorinae). Poeyana 184:1-17.

De La Cruz, J. 1978b. Composicion zoogeografica de la fauna de garrapatas (Acarina: Ixodoidea) de Cuba. Poeyana 185:1-5.

DeTray, D.F. 1957. African swine fever. A review. Bull. Epizo. Dis. Afr. 5:475-478.

DeTray, D.E. 1963. African swine fever. Adv. Vet. Sci. 8:299-333.

Dhanda, V. and P.K. Rajagopalan. 1971. Ornithodoros (Reticulinasus) chiropterphila, new species, (Acarina: Argasidae) a new bat ectoparasite from Mysore State, India. Oriental Insects 5:135-143.

Diab, F.M. and Z.R. Soliman. 1977. An experimental study of Borrelia anserina in four species of Argas ticks. 1. Spirochete localization and densities. Zeit. Parasitenk. 53:201-212.

Diemer, J.E. 1986. Gopher tortoise status and harvest impact determination. Unpublished Annual Performance Report, Florida Game and Freshwater Fish Commission. Tallahassee, FL.

Doube, B.M. 1975a. Two races of the kangaroo tick Ornithodoros (Pavlovskyella) gurneyi Warburton. J. Aust. Entomol. Soc. 14:329-332.

- Doube, B.M. 1975b. The biology of the kangaroo tick Ornithodoros (Pavlovskyella) gurneyi Warburton (Acarina: Argasidae), in the laboratory. J. Med. Entomol. 12:240-243.
- Duffy, D.C. 1983. The ecology of tick parasitism on densely nesting Peruvian seabirds. Ecology 64:110-119.
- Dunn, L.H. 1927. Notes on two species of South American ticks, Ornithodoros talaje Guerin-Mene. and Ornithodoros venezuelensis Brumpt. J. Parasitol. 13:177-182.
- †Eisenberg, J.F. 1983. The gopher tortoise as a keystone species. Pages 1-4 in R.J. Bryant and R. Franz (eds.). The gopher tortoise: a keystone species. Proc. 4th Ann. Mtg., Gopher Tortoise Council.
- El Shoura, S.M., H.Hoogstraal and M.A.Roshdy. 1984. Nuttalliella namaqua (Ixodoidea: Nuttalliellidae): female internal morphology. J. Parasitol. 70:114-120.
- Endris, R.G., T.M.Haslett, G.Geering, W.R.Hess and M.J.Monahan. 1986. Hemolymph test for the detection of African swine fever virus in soft ticks (Argasidae: Ornithodoros). J. Med. Entomol. (in press).
- Enright, J.B., D.E.Behymer, C.E.Franti, V.J.Dutson, W.M.Longhurst, M.E.Wright and J.E.Goggin. 1971. The behavior of Q fever rickettsiae isolated from wild animals in northern California. J. Wild. Dis. 7:83-90.
- Fearnhead, E.A. 1962. Investigation on the bionomics of Ornithodoros zumpti Heisch et Guggisberg (Ixodoidea: Argasidae). Zeit. Parasitenk. 22:114-117.
- Feldman-Muhsam, B. 1973. Autogeny in soft ticks of the genus Ornithodoros (Acari: Argasidae). J. Parasitol. 59:536-539.
- Feldman-Muhsam, B. and Y.Havivi. 1973. Autogeny in the tick Ornithodoros tholozani (Ixodoidea, Argasidae). J Med. Entomol. 10:185-189.
- Felsenfeld, O. 1971. Borrelia: Strains, Vectors, Human and Animal Borreliosis. W.H.Green, St. Louis, MO.

- Felsenfeld, O. 1974. Genus IV Borrelia Spellengoebel 1907, pages 184-190 in Bergey's Manual of Determinative Bacteriology. R.E.Buchanan and N.E.Gibbons, (eds.). Williams and Wilkins, Baltimore, MD.
- Felsenfeld, O. 1979. Borreliosis. pages 79-96 in CRC Handbook series in Zoonoses. Section A. Bacterial, Rickettsial and Mycotic Diseases. Volume I. Ed. J.H. Steele. CRC Press Inc., Boca Raton, Florida.
- Filippova, N.A. 1966. Argasid ticks (Argasidae). Fauna SSSR. Paukობრძნყე 4:1-225. (cited in Hoogstraal 1985)
- Fisher, R.A. and E.B.Ford. 1947. The spread of a gene in natural conditions in a colony of the moth Panaxia dominula L. Heredity 1:143-174.
- Fox, I. 1947. Ornithodoros puertoricensis, a new tick from rats in Puerto Rico. J. Parasitol. 33:253-259.
- Francis, E. 1938. Longevity of the tick Ornithodoros turicata and of Spirochaeta recurrentis within this tick. Publ. Health Rpts. 53:2220-2241.
- † Franz, P. 1986a. Gopherus polyphemus (Gopher-tortoise): Burrow commensals. Herp. Review 17:64.
- † Franz, P. 1986b. The Florida gopher frog and the Florida pine snake as burrow associates of the gopher tortoise in northern Florida. pages 16-20 in The gopher tortoise and its community. D.R. Jackson and R.J. Bryant (eds.) Proc. 5th Ann. Mgt. Gopher Tortoise Council. Gopher Tortoise Council, Anthony, Florida.
- Frolov, B.A. 1971. Study of seasonal diapause in females of fowl ticks (Argas persicus (Oken)). Tr. Vses. Nauchno. Issled. Inst. Vet. Sanit. 40:373-376. (in Russian) (cited in Khalil 1979)
- Gaber, M.S., G.M.Khalil, H.Hoogstraal and A.E.Aboul-Nasi. 1984. Borrelia crocidurae localization and transmission in Ornithodoros erraticus and O. savignyi. Parasitology 88:403-413.
- Geering, G., R.G.Endris, T.M.Haslett, P.L.Doroski and W.R.Hess. 1986. Identification of African swine fever viral antigens in the hemolymph of soft ticks (Argasidae; Ornithodoros) by the immunodot blot test. Amer. J. Trop. Med. 35:1027-1034.

- Geigy, R. 1968. Relapsing fevers. pages 175-216 in Infectious Blood Diseases of Man and Animals. Vol. II. D.Weinman and M.Ristic, (eds.). Academic Press, New York.
- George, J.E. and B.Cook. 1979. Exokinetic responses of Argas cooleyi and Ornithodoros concanensis (Acari: Ixodoidea: Argasidae) to various environmental temperatures. J. Med. Entomol. 16:275-285.
- Gibbs, E.P.J. 1981. Persistent viral infections of food animals: Their relevance to the international movement of livestock and germ plasm. Adv. Vet. Sci. & Comp. Med. 25:71-100.
- Gibbs E.P.J. and J.F.Putler. 1984. African swine fever-an assessment of risk for Florida. JAVMA 184:644-647.
- Gothe, R. 1984. Tick paralyses: Reasons for appearing during ixodid and argasid feeding. pages 199-223 in Current Topics in Vector Research. Vol. II. K.E.Harris, (ed.). Praeger, New York.
- Gothe, R and E.Koop. 1974. Zurbiologischer Bewertung der Validität von Argas (Persicargas) persicus (Oken, 1818), Argas (Persicargas) arboreus Kaiser, Hoogstraal und Kohls, 1964 and Argas (Persicargas) walkerae Kaiser und Hoogstraal, 1969. I. Untersuchungen zur Entwicklungsbiologie. Zeit. Parasitenk. 44:299-317. (cited in Kettle 1984)
- Gothe, R. and J.P.Kreier. 1977. Aegyptianella, Eperythiozoon and Haemobartonella pages 251-294 in Parasitic Protozoa Vol. 4. J.P.Kreier, (ed.). Academic Press, New York.
- Gothe, R., K.Kunze and H.Hoogstraal. 1979. The mechanisms of pathogenicity in the tick paralyses. J. Med. Entomol. 16:357-369.
- Gould, E.A., A.C.Chanas, A.Buckley and M.G.R.Varna. 1983. Immunofluorescence studies on the antigenic interrelationships of the Hughes virus serogroup (genus Nairovirus) and identification of a new strain. J. General Virol. 64:739-742.
- Gozony, L., E.Hindle and P.H.Ross. 1914. Serological test. J. Hygiene. 14:354-359.

- Greiner, E.C., P.P. Humphrey, R.C. Belden, W.B. Frankenberger, D.H. Austin and E.P.J. Gibbs. 1984. Ixodid ticks on feral swine in Florida. *J. Wildl. Dis.* 20:114-119.
- Groocock, C.M., W.R.Hess and W.J.Gladney. 1980. Experimental transmission of African swine fever virus by Ornithodoros coriaceus, an argasid tick indigenous to the United States. *Amer. J. Vet. Res.* 41:591-594.
- Guirgis, S.S. 1971. The subgenus Persicargas (Ixodoidea, Argasidae, Argas) 11. Ecology and seasonal dynamics of A. (P.) arboreus K¹⁵is, Hoogstraal and Kohls in Egypt. *J. Med. Entomol.* 8:407-414.
- Gunders, A.E. and A.Hadani. 1974. Transmission of a mammalian piroplasm by an argasid tick. *Nature* 247:225-226.
- Haberkorn, A. 1963a. Untersuchungen über das Verhalten von Ruckfallfieberspirochaeten insbesondere der Borrelia crocidurae - Gruppe in der Kleiderlaus (1. Teil) *Zeit. Trop. Parasitol.* 14:95-114.
- Haberkorn, A. 1963b. Untersuchungen über das Verhalten von Ruckfallfieberspirochaeten insbesondere der Borrelia crocidurae - Gruppe in der Kleiderlaus (2. Teil) *Zeit. Trop. Parasitol.* 14:209-239.
- Hafez, M., A.A.Abdel-Malek and S.S.Guirgis. 1971. The subgenus Persicargas (Ixodoidea, Argasidae, Argas). 12. Biological studies on the immature stages of A. (P.) arboreus Kaiser, Hoogstraal and Kohls in Egypt. *J. Med. Entomol.* 8:421-429.
- Hafez, M., A.A.Abdel-Malek and S.S.Guirgis. 1972. The subgenus Persicargas (Ixodoidea, Argasidae, Argas). 14. Biological studies on the adult stage of A. (P.) arboreus Kaiser, Hoogstraal and Kohls in Egypt. *J. Med. Entomol.* 9:19-29.
- 13
- Hallinan, T. 1927. Observations made in Duval County, northern Florida, on the gopher tortoise (Gopherus polyphemus). *Copeia* 14:11-20.
- 115
- Harbinson, C.F. 1937. The adobe tick on Gopherus agassizii. *Herpetologica* 1:80.

- Haresnape, J.M. and F.D.Mamu. 1986. The distribution of ticks of the Ornithodoros moubata complex (Ixodoidea, Argasidae) in Malawi and its relation to African swine fever epizootiology. J. Hygiene 96:535-544.
- Harwood, R.F. and M.T.James. 1979. Ticks and tick-associated diseases. pages 371-412 in Entomology in human and animal health. Macmillan Publ. Co. Inc., New York.
- Heisch, R.B. 1953. On a spirochaete isolated from Ornithodoros graingeri. Parasitology 43:133-135.
- Heisch, R.B. 1954a. The host of Ornithodoros grangeri.
Heisch and Guggisberg. 1952. E. African Med. J. 31:29.
- Heisch, R.B. 1954b. Ornithodoros moubata Murray in a porcupine burrow near Kitui. E. African Med. J. 31:483.
- Heisch, R.B. 1954c. Argas brumpti Neumann in the Kitui district of Kenya. E. African Med. J. 31:483-484.
- Hellman, K. and R.K.Hawkins. 1967. The action of tick extracts on blood coagulation and fibrinolysis. Thromb. Diath. Haemorrh. 18:617-625.
- Helmy, N., G.M.Khalil and F.Hoogstraal. 1983. Hyperparasitism in Ornithodoros erraticus. J. Parasitol. 69:229-233.
- Hess, W.R. 1971. African swine fever virus. Virol. Monogr. 9:1-33.
- Hess, W.R. 1981. African swine fever: a reassessment. Adv. Vet. Sci. & Comp. Med. 25:39-69.
- Hoffmann, A. 1962. Monografia de los Ixodoidea de Mexico. 1-Parte. Revista de la Sociedad Mexicana de Historia Natural. 23:191-307.
- Honzakova, E., V.Cerny and M.Daniel. 1983. The life cycle of Ornithodoros tadaridae Cerny and Dusbabek (Argasidae) under laboratory conditions. Folia Parasitol. 30:357-361.
- Hoogstraal, H. 1953a. Ornithodoros salahi sp. nov. (Ixodoidea, Argasidae) from the Cairo citadel, with notes on O. piriiformis Warburton, 1918 and O. batuensis Hirst, 1929. J. Parasitol. 39:256-263.

Hoogstraal, H. 1953b. Ornithodoros arenicolous sp. nov. (Ixodoidea, Argasidae) from Egyptian desert mammal burrows. J. Parasitol. 39:505-516.

Hoogstraal, H. 1955. Bat ticks of the genus Argas (Ixodoidea: Argasidae). 1. The subgenus Chiropterargas. Fieldiana Zool. 37:579-600.

Hoogstraal, H. 1956. African Ixodoidea. I. Ticks of the Sudan (with special reference to Equatoria Province and with Preliminary Reviews of the Genera Boophilus, Margaropus, and Hyalomma). Dept. of the Navy, Bureau of Medicine and Surgery, Washington D.C. 1101 pp.

Hoogstraal, H. 1957. Bat ticks of the genus Argas (Ixodoidea: Argasidae). 2. Secretargas new subgenus and A. transgaripepinus White, 1846, its adult and immature stages; with a definition of the subgenus Argas. Ann. Entomol. Soc. Amer. 50:544-549.

Hoogstraal, H. 1958. Bat ticks of the genus Argas (Ixodoidea: Argasidae). 3. The subgenus Carios, a redescription of A. (C.) vespertilionis (Latreille, 1802), and variation within an Egyptian population. Ann. Entomol. Soc. Amer. 51:19-26.

Hoogstraal, H. 1961. Migrating birds and their ectoparasites in relation to disease. E. Afr. Med. J. 38:221-226.

Hoogstraal, H. 1966. Ticks in relation to human diseases caused by viruses. Ann. Rev. Entomol. 11:261-308.

Hoogstraal, H. 1967. Ticks in relation to human diseases caused by Rickettsia species. Ann. Rev. Entomol. 12:377-420.

Hoogstraal, H. 1973a. Acarina (ticks) pages 89-103 in Viruses and Invertebrates. A.J.Gibbs, (ed.). North-Holland Publ. Co., Amsterdam.

Hoogstraal, H. 1973b. Viruses and ticks pages 349-390 in Viruses and Invertebrates. A.J.Gibbs (ed.). North-Holland Publ. Co., Amsterdam.

Hoogstraal, H. 1978. Biology of Ticks. pages 3-14 in Proceedings of an International Conference, Edinburgh, Sept.-Oct.1976. (Cited in Hoogstraal, 1985)

- Hoogstraal, H. 1979. Ticks and spirochetes. *Acta Tropica* 36:133-136.
- Hoogstraal, H. 1980. Established and emerging concepts regarding tick-associated viruses and unanswered questions. *Zent. Bakt. Parasit. Infek. Hyg. A. Suppl.* 9:49-63.
- Hoogstraal, H. 1981. Changing patterns of tickborne diseases in modern society. *Ann. Rev. Entomol.* 26:75-99.
- Hoogstraal, H. 1985. Argasid and Nuttalliellid Ticks as Parasites and Vectors. *Adv. Parasitol.* 24:135-238.
- Hoogstraal, H., C.M.Clifford and J.E.Keirans. 1973. Argas (Microargas) transversus (Ixodoidea: Argasidae) of Galapagos giant tortoises: Description of the female and nymph. *Ann. Entomol. Soc. Amer.* 66:727-732.
- Hoogstraal, H., C.M.Clifford and J.E.Keirans. 1979a. The Ornithodoros (Alectrobius) capensis group (Acarina: Ixodoidea: Argasidae) of the Palearctic and Oriental regions. O. (A.) coniceps identity, bird and mammal hosts, virus infections and distribution in Europe, Africa and Asia. *J. Parasitol.* 65:395-407.
- Hoogstraal, H., C.M.Clifford, J.E.Keirans, M.N.Kaiser and D.E.Evans. 1976. The Ornithodoros (Alectrobius) capensis group (Acarina: Ixodoidea: Argasidae) of the Palearctic and Oriental regions. O. (A.) maritimus, marine bird hosts, virus infections and distribution in Western Europe and northwestern Africa. *J. Parasitol.* 62:799-810.
- Hoogstraal, H., C.M.Clifford, J.E.Keirans and H.Y.Wassef. 1979b. Recent developments in biomedical knowledge of Argas ticks (Ixodoidea: Argasidae). pages 269-278 in *Recent Advances in Acarology*. Vol.II. J.G.Rodriguez, (ed.). Academic Press, New York.
- Hoogstraal, H., C.M.Clifford and M.A.Poshdy. 1984. The Haller's organ roof and anterior pit setae of Argas ticks (Ixodoidea: Argasidae). Subgenera Secretargas and Ogadenus. *J. Parasitol.* 70:403-406.
- Hoogstraal, H., C.M.Clifford, M.A.Roshdy and J.E.Keirans. 1983. The subgenus Persicargas (Ixodoidea: Argasidae: Argas). 38. Haller's organ roof and anterior pit setae in Persicargas and Microargas. *J. Parasitol.* 69:977-985. (Publ. in 1984)

- Hoogstraal, H. and M.D.Gallagher. 1982. Blister, pruritis and fever after bites by the Arabian tick Ornithodoros (Alectorobius) muesebecki. Lancet 8293:288-289.
- Hoogstraal, H., S.Kadarsan, M.N.Kaiser and P.F.D. van Peenen. 1974. Ornithodoros (Alectorobius) colloclaliae, new species (Ixodoidea: Argasidae) parasitizing cave swiftlets (Aves: Apodidae) in Java. Ann. Entomol. Soc. Amer. 67:224-230.
- Hoogstraal, H., M.W.Kaiser and G.M.Kohls. 1968. The subgenus Pericargas (Ixodoidea, Argasidae, Argas). 4. Argas (P.) robertsi, new species, a parasite of Australian fowl, and keys to Australian argasid species. Ann. Entomol. Soc. Amer. 61:535-539.
- Hoogstraal, H., M.N.Kaiser and H.E.McClure. 1975. The subgenus Persicargas (Ixodoidea: Argasidae: Argas). 20. A. (P.) robertsi parasitizing nesting wading birds and domestic chickens in the Australian and Oriental Regions, viral infections, and host migration. J. Med. Entomol. 11:513-524.
- Hoogstraal, H., M.N.Kaiser, J.B.Walker, J.A.Ledger, J.D.Converse and R.C.A.Rice. 1975. Observations on the subgenus Argas (Ixodoidea: Argasidae: Argas). 10. A. (A.) africolumbae, n. sp., a Pretoria virus-infected parasite of birds in southern and eastern Africa. J. Med. Entomol. 12:194-201.
- Hoogstraal, H. and K.C.Kim. 1985. Tick and mammal coevolution with emphasis on Haemaphysalis. pages 525-568 in Coevolution of Parasitic Arthropods and Mammals. K.C.Kim, (ed.). John Wiley and Sons, New York.
- Hoogstraal, H. and G.M.Kohls. 1960a. Observations on the subgenus Argas (Ixodoidea, Argasidae, Argas). 1. Study of A. reflexus reflexus (Fabricius, 1794), the European bird argasid. Ann. Entomol. Soc. Amer. 60:611-618.
- Hoogstraal, H. and G.M.Kohls. 1960b. Observations on the subgenus Argas (Ixodoidea, Argasidae, Argas). 3. A biological and systematic study of A. reflexus hermanni Audouin, 1827 (revalidated), the African bird argasid. Ann. Entomol. Soc. Amer. 60:743-755.

- Hoogstraal, H. and G.M.Kohls. 1966a. Ornithodoros (Pavlovskyella) macmillani new species (Ixodoidea: Argasidae) a nest parasite of Australian cockatoos (Kakatoe roseicapilla). Ann. Entomol. Soc. Amer. 59:86-92.
- Hoogstraal, H. and G.M.Kohls. 1966b. Argas (Microargas) transversus Banks (new subgenus) (Ixodoidea, Argasidae) a diminutive parasite of the Galapagos giant tortoise: Redescription of the holotype male and a description of the larva. Ann. Entomol. Soc. Amer. 59:247-252.
- Hoogstraal, H., D.E.Moorhouse, G.Wolf and H.Y.Wassef. 1977. Bat ticks of the genus Argas (Ixodoidea: Argasidae). A. (Carios) macrodermae, new species, from Queensland, Australia. Ann. Entomol. Soc. Amer. 70:861-870.
- Hoogstraal, H., R.M.Oliver and S.S.Guirgis. 1970. Larva, nymph and life cycle of Ornithodoros (Alectrobius) musesbecki (Ixodoidea: Argasidae), a virus-infected parasite of birds and petroleum industry employees in the Arabian Gulf. Ann. Entomol. Soc. Amer. 63:1762-1768.
- Hoogstraal, H., A.A.Salah and M.N.Kaiser. 1954. Summary of the known distribution and biology of Ornithodoros erraticus (Lucas, 1849) (Ixodoidea, Argasidae) in Egypt. J. Egypt. Publ. Health Assoc. 29:128-138.
- Hoogstraal, H., H.Y.Wassef, C.Hays and J.F.Keirans. 1985. Ornithodoros (Alectrobius) spheniscus n.sp. (Acarina: Ixodoidea: Argasidae: Ornithodoros (Alectrobius) capensis group), a tick parasite of the Humboldt penguin in Peru. J. Parasitol. 71:635-644.
- Hooker, W.A., F.C.Bishopp and H.P.Wood. 1912. The life history and bionomics of some North American ticks. USDA Bur. Entomol. Bull. 106. 238 pp.
- Hopla, C.E. 1955. Observations on the life history of the rabbit tick (Otobius lagophilus). J. Fan. Entomol. Soc. 28:114-116.
- Hopla, C.E. and J.E.Loya. 1983. The ectoparasites and microorganisms associated with cliff swallows in west-central Oklahoma. I. Ticks and Fleas. Bull. Soc. Vector Ecol. 8:111-121.

- Howden, H.F. 1963. Speculations on some beetles, barriers and climates during the Pleistocene and Pre-Pleistocene periods in some non-glaciated portions of North America. *Syst. Zool.* 12:178-201.
- Howden, H.F. 1966. Some possible effects of the Pleistocene on the distribution of North American Scarabaeidae (Coleoptera). *Can. Entomol.* 98:1177-1190.
- Howell, C.J., A.W.H. Neitz and D.J.J. Potgieter. 1975. Some toxic, physical and chemical properties of the oral secretion of the sand tampan Ornithodoros savignyi Audouin (1827). *Onderstepoort J. Vet. Res.* 42:99-102.
- Hubbard, H. G. 1894. The insect guests of the Florida land tortoise. *Insect Life* 6:302-315.
- Hubbard, H. G. 1896. Additional notes on the insect guests of the Florida land tortoise. *Proc. Entomol. Soc. Wash.* 3:299-302.
- Hubbell, T.N. and C. Goff. 1940. Florida pocket-gopher burrows and their arthropod inhabitants. *Proc. Fla. Acad. Sci.* 4:127-166.
- Hughes, L.F., C.M. Clifford, L.A. Thomas, H.A. Denmark and C.B. Philips. 1964. Isolation and characterization of a virus from soft ticks (Ornithodoros capensis group) collected on Bush Key, Dry Tortugas, Florida. *Amer. J. Trop. Med. Hyg.* 13:118-122.
- Humphrey, S.R., J.F. Eisenberg and R. Franz. 1985. Possibilities for restoring wildlife of a longleaf pine savanna in an abandoned citrus grove. *Wildl. Soc. Bull.* 13:487-496.
- Johnson, P.T. and J.N. Layne. 1961. A new species of Polygenis Jordan from Florida with remarks on its host relationships and zoogeographic significance (Siphonaptera: Rhopalosyllidae). *Proc. Entomol. Soc. Wash.* 63:115-123.
- Jones, E.K. and C.M. Clifford. 1972. The systematics of the subfamily Ornithodorinae (Acarina: Argasidae). V. A revised key to larval Argasidae of the Western Hemisphere and description of seven new species of Ornithodoros. *Ann. Entomol. Soc. Amer.* 65:730-740.

- Justines, G. and M.L.Kuns. 1970. Matucare virus, a new agent recovered from Ornithodoros (Alectorobius) boliviensis. Amer. J. Trop. Med. Hyg. 19:697-702.
- Kaiser, M.N. 1966a. The subgenus Persicargas (Ixodoidea, Argasidae, Argas) 3. The life cycle of A. (P.) arboreus, and a standardized rearing method for argasid ticks. Ann. Entomol. Soc. Amer. 59:496-502.
- Kaiser, M.N. 1966b. Viruses in ticks. I. Natural infections of Argas (Persicargas) arboreus by Quaranfil and Nyamanini viruses and absence of infections in A. (P.) persicus in Egypt. Amer. J. Trop. Med. Hyg. 15:964-975.
- Kaiser, M.N. 1966c. Viruses in ticks. II. Experimental transmission of Quaranfil virus by Argas (Persicargas) arboreus and A. (P.) persicus. Amer. J. Trop. Med. Hyg. 15:975-985.
- Kaiser, M.N. and H.Hoogstraal. 1973. Bat ticks of the genus Argas (Ixodoidea: Argasidae). 9. A. (Carios) daviesi, new species, from Western Australia. Ann. Entomol. Soc. Amer. 66:423-428.
- Kaiser, M.N. and H.Hoogstraal. 1974. Bat ticks of the genus Argas (Ixodoidea: Argasidae) 9. A. (Carios) dewae, new species, from Southeastern Australia and Tasmania. Ann. Entomol. Soc. Amer. 67:231-237.
- Kaiser, M.N. and H.Hoogstraal. 1975. Observations on the subgenus Argas (Ixodoidea: Argasidae: Argas). A. (A.) lowryae, new species, parasitizing cave-dwelling kestrels in the Nullarbor region of Western Australia. Ann. Entomol. Soc. Amer. 68:585-590.
- Kaiser, M.N., H.Hoogstraal and K.O.Horner. 1970. The subgenus Persicargas (Ixodoidea: Argasidae, Argas) 10. A. (P.) streptopelia, new species, a widely distributed parasite of resident and migrating doves in Africa and Cyprus, and epidemiological considerations. Ann. Entomol. Soc. Amer. 63:799-807.
- Kaiser, M.N., H.Hoogstraal and G.M.Kohls. 1964. The subgenus Persicargas, new subgenus (Ixodoidea, Argasidae, Argas). 1. A. (P.) arboreus, new species, an Egyptian persicus-like parasite of wild birds with a redefinition of the subgenus Argas. Ann. Entomol. Soc. Amer. 57:60-69.

- Kamil, S. and S.Bilal. 1938. Experimental research on the etiology of tularemia in Turkey. *Ann. Parasitol.* 16:530-542.
- Keirans, J.E. and C.M.Clifford. 1975. Nothaspis reddelli, new genus and new species (Ixodoidea: Argasidae), from a bat cave in Mexico. *Ann. Entomol. Soc. Amer.* 68:81-85.
- Keirans, J.E., C.M.Clifford and J.M.Capriles. 1971. Argas (Argas) dulus, new species (Ixodoidea: Argasidae), from nests of the palm chat, Dulus dominicus in the Dominican Republic. *Ann. Entomol. Soc. Amer.* 64:1410-1413.
- Keirans, J.E., C.M.Clifford and H.Hoogstraal. 1980. Identity of the nymphs and adults of the Galapagos iguanid lizard parasites Ornithodoros (Alectrobius) darwini and O. (A.) galapagensis (Ixodoidea: Argasidae). *J. Med. Entomol.* 17:427-438.
- Keirans, J.E., C.M.Clifford and H.Hoogstraal. 1984. Ornithodoros (Alectrobius) yunkeri, new species (Acarina: Ixodoidea: Argasidae), from seabirds and nesting sites in the Galapagos Islands. *J. Med. Entomol.* 21:344-350.
- Keirans, J.E., C.M.Clifford, H.Hoogstraal and E.R.Easton. 1976. Discovery of Nuttalliella namaqua Bedford (Acarina: Ixodoidea: Nuttalliellidae) in Tanzania and redescription of the female based on scanning electron microscopy. *Ann. Entomol. Soc. Amer.* 69:926-932.
- Keirans, J.E., H.Hoogstraal and C.M.Clifford. 1977a. Ornithodoros (Proknekalia) vansomeri, new subgenus and new species (Acarina: Ixodoidea: Argasidae), a swallow nest parasite in Kenya. *Ann. Entomol. Soc. Amer.* 70:221-228.
- Keirans, J.E., C.M.Clifford and J.R.Reddell. 1977b. Description of the immature stages of Nothaspis reddelli (Ixodoidea: Argasidae) from bat caves in Mexico. *Ann. Entomol. Soc. Amer.* 70:591-595.
- Keirans, J.E., F.J.Radovsky and C.M.Clifford. 1973. Argas (Argas) monachus, new species (Ixodoidea: Argasidae), from hosts of the monk parakeet, Myropsitta monachus in Argentina. *J. Med. Entomol.* 10:511-516.

- Kemp, D.H., B.F.Stone and K.C.Binnington. 1982. Tick attachment and feeding: Role of mouthparts, feeding apparatus, salivary gland secretions and the host response. pages 119-168 in Physiology of Ticks. F.D.Obenchain and R.Galun, (eds.). Pergamon Press, New York.
- Kemp, H.A., W.H.Moursund and H.E.Wright. 1934. Relapsing fever in Texas. IV. Ornithodoros turicata Duges; A vector of the disease. Amer. J. Trop. Med. 14:479-487.
- Kettle, D.S. 1984. Medical and Veterinary Entomology. John Wiley and Sons, New York. 658 pp.
- Khalil, G.M. 1979. The subgenus Persicargas (Ixodoidea: Argasidae: Argas) 31. The life cycle of A. (P.) persicus in the laboratory. J. Med. Entomol. 16:200-206.
- Khalil, G.M. and H.Hoogstraal. 1981. The life cycle of Ornithodoros (Alectrobius) amblus (Acarina: Ixodoidea: Argasidae) in the laboratory. J. Med. Entomol. 18:134-139.
- Khalil, G.M., H.Hoogstraal and J.H.Oliver Jr. 1980. Biological evaluation of the systematic validity of the African Argas (Persicargas) arboreus and the Asian-Australian A. (P.) robertsi (Ixodoidea: Argasidae). Intl. J. Parasitol. 10:253-259.
- Khalil, G.M. and S.A.Metwally. 1974. Observations on the subgenus Argas (Ixodoidea: Argasidae: Argas). 8. The life cycle of A. (A.) hermanni. J. Med. Entomol. 11:355-362.
- Kilbourne, A. I. 1981. Temperature preference testing of Ornithodoros turicata (Acarina: Ixodoidea: Argasidae). (unpublished manuscript)
- King, J.A. (ed.). 1968. Biology of Peromyscus (Rodentia). Special publication No. 2., Amer. Soc. of Mammalogists.
- Kitaoka, S. and H.Suzuki. 1973. Ornithodoros (Alectrobius) sawaii sp. n. (Ixodoidea, Argasidae) associated with the streaked shearwater Colonectris leucomelas, from the Amami-oshima Islands, Japan. Natl. Inst. Anim. Health Quart. Tokyo 13:142-148.
- Kohls, G.M. and C.M.Clifford. 1963. Ornithodoros sparnus sp.n. a parasite of wood rats Neotoma spp. and deer mice Peromyscus spp. in Utah and Arizona. J. Parasitol. 49:857-861.

- Kohls, G.M., C.M.Clifford and E.K.Jones. 1969. The systematics of the subfamily Ornithodorinae (Acarina: Argasidae). IV. Eight new species of Ornithodoros from the Western Hemisphere. Annals of the Entomol. Soc. Amer. 62:1035-1043.
- Kohls, G.M. and H.Hoogstraal. 1962. Bat ticks of the genus Argas (Ixodoidea, Argasidae) 4. A. (Carios) australiensis n. sp. from Australia. Ann. Entomol. Soc. Amer. 55:555-559.
- Kohls, G.M., H.Hoogstraal and C.M.Clifford. 1961. Observations on the subgenus Argas (Ixodoidea, Argasidae, Argas). 5. Study of A. brevipes 1908, from birds in Arizona and California, USA and Baja California, Mexico. Ann. Entomol. Soc. Amer. 54:869-877.
- Kohls, G.M., H.Hoogstraal, C.M.Clifford and M.N.Kaiser, 1970. The subgenus Persicargas (Ixodoidea, Argasidae, Argas). 9. Redescription and New World records of Argas (P.) persicus (Oken) and resurrection, redescription and records of A. (P.) radiatus Railliet, A. (P.) sanchezii Duges and A. (P.) miniatus Koch, New World ticks misidentified as A. (P.) persicus. Ann. Entomol. Soc. Amer. 63:590-606.
- Kohls, G.M., D.E.Sonenshine and C.M.Clifford. 1965. The systematics of the subfamily Ornithodorinae (Acarina: Argasidae). II. Identification of the larvae of the Western Hemisphere and descriptions of three new species. Ann. Entomol. Soc. Amer. 58:331-364.
- Kraiss, A. and R.Gothe. 1982. The life cycle of Argas (Argas) africolumbae under constant abiotic and biotic conditions. Vet. Parasitol. 11:365-373.
- Kranz, G.W. 1978. A Manual of Acarology. 2nd Ed. Oregon State University, Corvallis, Oregon. 509pp.
- Kurz, H. 1942. Florida dunes and scrub, vegetation and geology. Fla. Geol. Surv., Geol. Bull. 23:1-154.
- Kusov, V.N. 1973. Ornithodorinae ticks of Kazakhstan and republics of Central Asia. Inst. Zool. Akad. Nauk Kaz. SSR Alma-Ata (cited in Hoogstraal 1985).
- Kusov, V.N., S.A.Amanzhulov and O.V.Postricheva. 1962. On the problem of Q fever infections in the genus Ornithodoros. Paraz. Sel-skikh. Zhiv. Kaz. 1:229-235. (English translation: NAMRU3T85)

- Laessle, A.M. 1958. The origin and sucessional relationship of sandhill vegetation and sand-pine scrub. *Ecol. Monogr.* 28:361-387.
- Lane, R.S., W.Burgdorfer, S.F.Hayes and A.G.Barbour. 1985. Isolation of a spirochete from the soft tick Ornithodoros coriaceus: A possible agent of epizootic bovine abortion. *Science* 230:85-87.
- Lavoipierre, M.M.J. and R.F.Rick. 1955. Observations on the feeding habits of argasid ticks and the effect of their bites on laboratory animals, together with a note on the production of coxal fluid by several of the species studied. *Ann. Trop. Med. Parasitol.* 49:96-113.
- Layne, J.N. 1963. A study of the parasites of the Florida mouse Peromyscus floridanus in relation to host and environmental factors. *Tulane Stud. Zool.* 11:3-27.
- Leahy, M.G. 1979. Pheromones of argasid ticks. pages 297-308 in *Recent Advances in Acarology Vol. II.* J.G. Rodriguez (ed.) Academic Press, New York.
- Loomis, E.D. 1961. Life histories of ticks under laboratory conditions (Acarina: Ixodidae and Argasidae). *J. Parasitol.* 47:91-99.
- Loomis, E.C., E.T.Schmidtman and M.N.Oliver. 1974. A summary review on the distribution of Ornithodoros coriaceus Koch in California (Acarina: Argasidae). *Cal. Vect. Views* 21:57-63.
- L'vov, D.K., M.A.Kostyukov, T.P.Pak and V.L.Gromashevsky. 1980. Isolation from the blood of a sick person of an arbovirus antigenically related to Issyk-Kul virus. *Voprosy Virusologii* 25:61-62. (English translation: NAMRU3 T1442)
- L'vov, D.K., G.N.Leonova, V.L.Gromashevsky, T.M.Skvortsova, A.A.Timofeeva, A.A.Sazonov, Y.G.Gofman, L.K.Berezina, S.M.Klimenko and V.A.Zakaryan. 1975b. New arboviruses from encephalomyocarditis group, Bunyam-viridal and ungrouped arboviruses isolated in the far east of the USSR. *International Virology, Abstract of 3rd International Congress for Virology, Madrid, Sept. 3.* 192 pp. (cited in Hoogstraal 1985)

- L'vov, D.K., V.M.Neronov, V.L.Gromashevsky, T.M.Skvortsova, L.K.Berezina, G.A.Sidorova, Z.M.Zhmaeva, Y.A.Gofman, S.M.Klimenko and K.B.Fomina. 1976. "Karshi" virus a new flavivirus (Togaviridae) isolated from Ornithodoros papillipes (Birula 1895) ticks in Uzbek SSR. Arch. Virol. 50:29-36.
- L'vov, D.K., G.A.Sidorova, V.L.Gromashevsky, T.M.Skvortsova, L.K.Berezina, N.G.Kondrashina and A.U.Uralov. 1979. Chim virus, a new arbovirus isolated from ixodid and argasid ticks collected in burrows of great gerbils in Uzbek SSR. Voprosy Virusologii 24:286-289. (In Russian, English translation NAMRU3 T1408).
- L'vov, D.K., A.A.Timofeeva, V.A.Smirnov, V.L.Gromashevsky, G.A.Sidorova, L.P.Nikiforov, A.A.Sazonov, A.P.Andreev, T.M.Skvortsova, L.K.Berezina and V.A.Aristova. 1975a. Ecology of tick-borne viruses in colonies of birds in the USSR. Med. Biol. 53:325-330.
- L'vov, D.K., Y.M.Tsirkov, F.R.Karas, E.M.Timofeev, V.L.Gromashevsky, O.V.Veselovskaya, N.Z.Osipova, K.B.Fomina and Y.I.Grebenyuk. 1973. "Sokuluk" virus, a new group B arbovirus isolated from Vespertilio pipistrellus Schreber 1775, bat in the Kirghiz SSR. Arch. Ges. Virusforsch 41:170-174.
- Malkova, D., J.Holubova, V.Cerny, M.Daniel, A.Fernandez, J.La Cruz, M.Herrera and C.H.Calisher. 1985. Estero Real virus: a new virus isolated from argasid ticks Ornithodoros tadaridae in Cuba. Acta Virol. 29:247-250.
- Manso Ribeiro, J., Nunes Petisca, J.L., Lopes Frazao, F. and Sobral, M. 1963. Vaccination against ASF. Bull. Off. Int. Epiz. 60:921-937. (cited in Wardley et al. 1983)
- Marx, G. 1895. (In anonymous obituary.) Proc. Entomol Soc. Wash. 3:195-201.
- Mathews, R.E.F. 1979. Classification and nomenclature of viruses. Intervirology 12:129-296.
- Mayer, M. 1918. Über den Dauerparasitismus von Schizotrypanum cruzi bei Ornithodoros moubata. Arch. Schiffs. U. Tropenhyg. 22:158-160. (cited in Hoogstraal 1956)

McKercher, D.G., G.L.Crenshaw, J.H.Theis, E.M.Wada and C.M.Mauris. 1973. Experimentally induced immunity to chlamydial abortion of cattle. *J. Infect. Dis.* 128:231-234.

McKercher, D.G., E.A.Robinson, E.M.Wada, J.K.Saito and C.E.Frantl. 1969. Vaccination of cattle against epizootic bovine abortion. *Cornell Vet.* 59:211-226.

McKercher, D.G., E.M.Wada, S.K.Ault and J.H.Theis. 1980. Viral agents recovered from Ornithodoros coriaceus, a vector of epizootic bovine abortion. *Amer. J. Vet. Res.* 41:803-805.

Medley, J.G. and E.H.Ahrens. 1968. Fluorescent dyes for marking and recovering fowl ticks in poultry houses treated with insecticides. *J. Econ. Entomol.* 61:81-84.

Medley, J.G. and E.Ahrens. 1970. Life history and bionomics of two American species of fowl ticks (Ixodoidea, Argasidae, Argas) of the subgenus Persicargas. *Ann. Entomol. Soc. Amer.* 63:1591-1594.

Mellor, P.S. and P.J.Wilkinson. 1985. Experimental transmission of African swine fever virus by Ornithodoros savignyi (Audouin). *Res. Vet. Sci.* 39:353-356.

Miadonna, A., A.Tedeschi, E.Leggieri, P.Falagiani, M.Nazzari, M.Manconi and C.Zanussi. 1982. Anaphylactic shock caused by allergy to the venom of Argas reflexus. *Ann. Allergy* 49:293-295.

Miller, B.R., R.Loomis, A.Dejean and H.Hoogstraal. 1985. Qalyub virus (Bunyaviridae: Nairovirus) replication in the tick Ornithodoros (Pavlovskyella) erraticus. *Amer. J. Trop. Med. Hyg.* 34:180-187.

Miller, R.B. and L.A. Stange. 1983. The ant-lions of Florida, Glenurus gratus (Say) (Neuroptera: Mymeleontidae). *FL Dept. Agr. & Consumer Serv., Div. Plant Industry. Entomol. Circ.* 251:1-2.

+ Milstrey, E.G. 1986. Ticks and invertebrate commensals in gopher tortoise burrows: Implications and importance. pages 4-15 in The gopher tortoise and its community. *Proc. 5th Ann. Mtg. Gopher Tortoise Council.* (D.R. Jackson and R.J. Bryant (eds.)). *Gopher Tortoise Council, Antony, FL.*

- Mirzoeva, N.M., Z.L.Sultanova, I.G.Kanbai, V.R.Obukhova, S.Y.Gaidamovich, E.I.Sokolova and N.M.Kulieva. 1974. Biological properties of West Nile virus strains isolated in Azerbaijan. pages 119-123 in Arboviruses. S.Y.Gaidamovich, (ed.). Akad. Med. Nauk SSR. Moscow. (English translation: NAMRU3 T1159)
- Montgomery, R.E. 1921. On a form of swine fever occurring in British East Africa (Kenya Colony). J. Comp. Path. 34:159-191, 243-262.
- Moore, J.C. 1953. The fox squirrel in Florida: Variation and natural history. Unpublished PhD. dissertation. Univ. of Florida, Gainesville, Florida.
- Moulton, F.R.(ed.) 1942. A symposium on relapsing fever in the Americas. Dallas, Texas. Dec. 30-31,1941. Amer. Assoc. Adv. Sci. Smithsonian Inst., Bldg. No. 18., Washington, DC. 130 pp.
- Nuttall, G.H.F. and C.Strickland. 1908. On the presence of an anticoagulin in the salivary glands and intestines of Argas persicus. Parasitology 1:302-310.
- Nuttall, G.H.F. and C.Warburton. 1908. Ticks, a monograph of the Ixodoidea. Part I. Argasidae. Cambridge University Press, London. 104+35 pp.
- Obenchain, F.D. and R.Galun. 1982. Preface. pages vii-ix in Physiology of Ticks. F.D. Obenchain and R.Galun, (eds.). Pergamon Press Ltd., Oxford, England. (Publ. in 1983).
- Oliver, J.H. Jr. 1977. Cytogenetics of mites and ticks. Ann. Rev. Entomol. 22:407-429.
- Oliver, J.H. and R.L.Osburn. 1977. Cytogenetics of ticks (Acari: Ixodoidea). 15. Notes on chromosomes and maturation of Otobius megnini and Otobius lagophilus. J. Parasitol. 63:176-178.
- Osebold, J.W., R.Spezialetti, M.B.Jennings, R.F.Pritchett and R.B.Bushnell. 1986. Congenital spirochetosis in calves: Association with epizootic bovine abortion. J. Amer. Vet. Med. Assoc. 188:371-376.
- Patton, W.S. and F.W.Craig. 1913. A textbook of medical entomology. Christian Literature Society for India. London, Madras and Calcutta. 768 pp. (cited in Hoogstraal 1956)

Pavlovskii, E.N. 1960. Present theory on natural focality of human diseases, pages 6-40 in Human diseases with natural focality. Moscow.

Pavlovskii, E.N. and A.N.Skrynnik. 1959. Laboratory observations on the tick Ornithodoros hermsi Wheeler, 1935. Dokl. Akad. Nauk SSR 128:879-881.

Pavlovskii, E.N. and A.N.Skrynnik. 1960. Comparative data on the biology of some species of ticks of the genus Ornithodoros. Dokl. Akad. Nauk SSR 133:734-736.

Peacock, P.B. 1958. Tick paralysis or poliomyelitis. So. Afr. J. Med. Sci. 32:201-202.

Peirce, M.A. 1974. Distribution and ecology of Ornithodoros moubata porcina Walton (Acarina) in animal burrows in East Africa. Bull. Ent. Res. 64:605-619.

Philip, C.B. and L.E.Roseboom. 1973. Medico-Veterinary Entomology: A generation in progress. pages 333-360 in History of Entomology. R.F.Smith, T.E.Mittler and C.N.Smith, (eds.). Annual Review Inc., Palo Alto, CA.

Philip, R.N., E.A.Casper, R.L.Anacks, J.Cory, S.F.Hayes, W.Burgdorfer and C.E.Yunker. 1983. Rickettsia bellii sp. nov.: A tick-borne rickettsia widely distributed in the United States, that is distinct from the spotted fever and typhus biogroups. Intl. J. Syst. Bact. 33:94-106.

Pini, A. 1976. Isolation and segregation of non-hemadsorbing strains of ASF. Vet. Rec. 99:479-480.

Plowright, W. 1975. African Swine Fever (ASF). pages 82-82 in International catalog of arboviruses including certain viruses of vertebrates. Trygve O. Berge, (ed.). DHEW (CDC) 75-8301. 789 pp.

Plowright, W. 1977. Vector transmission of African swine fever. Seminar on Hog Cholera/classical swine fever and ASF. Comm. Eur. 5904EN: 575-587.

Plowright, W., J.Parker and M.A.Peirce. 1969. African swine fever virus in ticks (Ornithodoros moubata Murray) collected from animal burrows in Tanzania. Nature 221:1071-1073.

- Plowright, W., C.T.Perry and A.Greig. 1974. Sexual transmission of ASFV in the tick Ornithodoros moubata porcinus, Walton. Res. Vet. Sci. 17:106-113.
- Plowright, W., C.T.Perry and M.A.Pierce. 1970. Transovarial infection with ASFV in the Argasid tick Ornithodoros moubata porcinus, Walton. Res. Vet. Sci. 11:582-584.
- Pospelova-Shtrom, M.V. 1946. On the Argasidae system (with description of two new subfamilies, three new tribes and one new genus). Med. Parasitologia Parasitarn. Bolesni. 15:47-58.
- Pospelova-Shtrom, M.V. 1953. Ornithodorinae ticks and their epidemiological significance. MEDG12., Moscow. 236
- Pospelova-Shtrom, M.V. 1969. On the system of classification of ticks of the family Argasidae. Can. 1890. Acarologia 11:1-22.
- Pound, J.M., J.D.Campbell, R.H.Andrews and J.H.Oliver Jr. 1986. The relationship between weight of nymphal stages and subsequent development of Ornithodoros parkeri (Acari, Argasidae). J. Med. Entomol. 23:320-325.
- Rau, U.R. and K.N.A.Rao. 1971. Ornithodoros (O.) indica sp.n. (Ixodoidea: Argasidae), a parasite of the barking deer in the north-east frontier agency of India. J. Parasitol. 57:432-435.
- Rehacek, J., J.Urvolgyi and E.Kovacova. 1977. Massive occurrence of rickettsia of the spotted fever group in fowl tampan Argas persicus in the Armenian SSR. Acta Virol. (Prague) 21:431-438.
- Robson, D.S. and H.A. Regier. 1964. Sample size in Peterson mark recapture experiments. Trans. Amer. Fish. Soc. 93:215-226.
- Roff, D.A. 1973. An examination of some statistical tests used in the analysis of mark-recapture data. Oecologia 12:35-54.
- Rohdendorf, B.D. (ed.) 1962. Foundations of Paleontology. Arthropods, tracheates and chelicerates. Publications of the Academy of Science, Moscow. 560 pp. (in Russian) (cited in Harwood and James, 1974).

- Rosenstein, M. 1976. Paralysis in chickens caused by larvae of the poultry tick Argas persicus. Avian Dis. 20:407-409.
- Roshdy, M.A. 1961. Comparative internal morphology of subgenera of Argas ticks (Ixodoidea, Argasidae) 1. Subgenus Carios: Argas vespertilionis (Latreille, 1802) J. Parasitol. 47:987-994.
- Roshdy, M.A. 1962. Comparative internal morphology of subgenera of Argas ticks (Ixodoidea, Argasidae) 2. Subgenus Chiropterargas: Argas boueti. Roubaud and Colas-Belcour, 1933. J. Parasitol. 48:623-630.
- Roshdy, M.A. 1963. Comparative internal morphology of subgenera of Argas ticks (Ixodoidea: Argasidae). 3. Subgenus Secretargas: Argas transgaripepinus, White, 1846. J. Parasitol. 49:851-856.
- Roshdy, M.A. and H.Hoogstraal. 1974. Bat ticks of the genus Argas (Ixodoidea, Argasidae) 11. The structure and possible function of the ventral paired grooves in A. (Chiropterargas) boueti and A. (Carios) vespertilionis. Zeit. Parasitenk. 44:15-18.
- Roshdy, M.A., H.Hoogstraal, A.A.Banaja and S.M. El Shoura. 1983. Nuttalliella namagua (Ixodoidea: Nuttalliellidae): Spiracle structure and surface morphology. Zeit. Parasitenk. 69:817-821.
- Roshdy, M.A., H.Hoogstraal, C.M.Clifford, J.E.Keirans and M.D.Corwin. 1984. Bat ticks of the genus Argas (Ixodoidea: Argasidae). 13. Haller's organ roof and anterior pit setae in Carios and Chiropterargas. J. Parasitol. 70:407-411.
- Ryckman, R.E. and G.M.Kohls. 1962. The desert tortoise, Gopherus agassizii, a host for the tick Ornithodoros turicata in California. J. Parasitol. 48:502-503.
- St. George, T.D., H.H.Standfast, R.L.Doherty, J.G.Carley, C.Fillipich and J.Brandsma. 1977. The isolation of Samarez Reef virus, a new flavivirus, from bird ticks Ornithodoros capensis and Ixodes eudyptidis in Australia. Aust. J. Exp. Biol. Med. Sci. 55:493-499.

St. George, T.D., D.H.Cybinsky, A.J.Main, N.McKilligan and D.H.Kemp. 1984. Isolation of a new arbovirus from the tick Argas robertsi from a cattle egret, Bubulcus ibis coromandus, colony in Australia. Aust. J. Biol. Sci. 37:85-89.

Sanchez Botija, C. 1963. Reservorios del virus de la peste porcine africana. Investigacion del virus de la P.P.A. en los arthropodos mediante la prueba de la hemadsorcion. Bull. Off. Intl. Epiz. 60:895-899. (cited in Wardley et al. 1983)

Santos, S.M. 1982. O combate ao carrapato das aves. Estado de Sao Paulo Supl. Agricola 5.

Scott, G.R. 1965. The virus of African swine fever and its transmission. Bull. Off. Intl. Epiz. 63:645-677.

Schmidt, J.R. and M.I.Said. 1964. Isolation of West Nile virus from the African bird argasid, Argas reflexus hermanni, in Egypt. J. Med. Entomol. 1:83-86.

Schmidtman, E.T., R.B.Bushnell, E.C.Loomis, M.N.Oliver and J.H.Theis. 1976. Experimental and epizootic evidence associating Ornithodoros coriaceus Koch (Acari: Argasidae) with the exposure of cattle to epizootic bovine abortion in California. J. Med. Entomol. 13:292-299.

Sidorova, G.A., D.K.L'vov, V.L.Gromashevsky and V.P.Andreev 1975. Landscape associations of some virus foci in Central Asia. pages 50-51 in Ecology of Viruses. D.K.L'vov and I.S.Sattarov, (eds.). Akad. Med. Nauk SSR., Moscow. (English translation: NAMRU3 T1133)

Singer, F.J., D.K.Otto, A.R.Fipton and C.P.Hable. 1981. Home ranges, movements and habitat use of European wild boar in Tennessee. J. Wildl. Management 45:343-353.

Singh, K.R.P., M.K.Goverdhan and U.K.M.Bhat. 1971. Transmission of Kyasanur forest disease virus by soft tick, Argas persicus (Ixodoidea: Argasidae). Ind. J. Med. Res. 59:213-218.

Siuda, K., H.Hoogstraal, C.M.Clifford and H.Y.Wassef. 1979. Observations on the subgenus Argas (Ixodoidea: Argasidae: Argas). 17. Argas (A.) polonicus sp. n. parasitizing domestic pigeons in Krakow, Poland. J. Parasitol. 65:170-181.

- Smith, D.J.W. 1942. Studies in the epidemiology of Q fever. II. Experimental infection of the ticks Haemaphysalis bispinosa and Ornithodoros sp. with Rickettsia burneti. Aust. J. Exp. Biol. Med. Sci. 20:295-296.
- Smith, T. and F.L.Kilborne. 1893. Investigations into the nature, causation and prevention of Texas or southern cattle fever. USDA Bur. Anim. Indust. Bull. 1:1-301.
- Sonenshine, D.E. and G.Anastos. 1960. Observations on the life history of the bat tick Ornithodoros kelleyi (Acarina: Argasidae). J. Parasitol. 46:449-454.
- Sonenshine, D.E., C.M.Clifford and G.M.Kohls. 1962. The identification of larvae of the genus Argas (Acarina: Argasidae). Acarologia 4:193-214.
- Sonenshine, D.E., C.M.Clifford and G.M.Kohls. 1966. The systematics of the subfamily Ornithodorinae (Acarina: Argasidae). III. Identification of the larvae of the Eastern Hemisphere. Ann. Entomol. Soc. Amer. 59:92-122.
- Sreenivasan, M.A., H.R.Phat, C.N.Dandawate and A.S.Malukjkar. 1983. Muroor virus, a new arbovirus isolated in India from the bat tick Ornithodoros piriformis. Indian J. Med. Res. 78:295-299.
- Steere, A.C., S.E.Malawista, J.E.Craft, D.K.Fisher and M.Garcia-Blanco, (eds.). 1984. First International Symposium on Lyme disease. Yale University School of Medicine, Nov. 16-18, 1983. Yale J. Biol. Med. 57:447-713.
- Stone, S.S. and Hess, W.R. 1965. Separation of virus and soluble non-infectious antigens in ASFV. Amer J. Vet. Res. 28:475-481.
- Storz, J., D.G.McKercher, J.A.Howarth and O.C.Staub. 1960. The isolation of a viral agent from epizootic bovine abortion. J. Amer. Vet. Med. Assoc. 137:509-514.
- Strickland, G.T. 1984. Hunter's tropical medicine 6th ed. W.B. Saunders Co., Philadelphia, PA. 1057pp.
- Suitor, E.C. Jr. 1964. The relationship of Wolbachia persicus Suitor and Weiss to its host. J. Insect Path. 6:111-124.

Suitor, E.C. Jr. and E.Weiss. 1961. Isolation of a rickettsia-like microorganism (Wolbachia persicus n. sp.) from Argas persicus Oken. J. Infect. Dis. 108:95-106.

Sureau, P., J.M.Klein, J.Casals, J.P.Digoutte, J.J.Salaun, N.Piazak and M.A.Calvo. 1980. Isolement des virus Thogoto, Wad Medani, Wanowrie et de la fièvre hémorragique de Crimée-Congo en Iran à partir de tiques d'animaux domestiques. Ann. Inst. Pasteur Ser. Virol. 131E:185-200. (cited in Hoogstraal 1985)

Takahashi, M., C.E.Yunker, C.M.Clifford, W.Nakano, F.Fujino, K.Tanifiyi and L.A.Thomas. 1982. Isolation and characterization of Midway virus: a new tick-borne virus related to Nymanini. J. Med. Virol. 10:181-193.

Thomson, G.R. 1985. The epidemiology of African swine fever: The role of free living hosts in Africa. Onderstepoort J. Vet. Res. 52:201-209.

Thomson, G.R., M.D.Gainaru and A.F. van Dellan. 1980. Experimental infection of warthog (Phacochoerus aethiopicus) with ASFV. Onderstepoort J. Vet Res. 47:19-22.

Trager, W. 1940. A note on the problem of acquired immunity to argasid ticks. J. Parasitol. 26:71-74.

Van de Merwe, S. 1968. Some remarks on the 'tampans' of the Ornithodoros moubata complex in Southern Africa. Zool. Anz. 181:280-289. (cited in Peirce 1974)

Vasileva, I.S. 1976a. Habitats of Ornithodoros tartakowski, Argasidae, populations in the south Tadzhik SSR, USSR. Part 1. Prevalence of ticks in different types of burrows. Med. Parazit. Para. Bol. 45:42-49.

Vasileva, I.S. 1976b. Habitats of Ornithodoros tartakowski OL. (Argasidae) along the pathways of burrows in the summer. Med. Parazit. Para. Bol. 45:204-209.

Wada, I.M., D.G.McKercher, G.Castrucci and J.H.Theis. 1976. Preliminary characterization and pathogenicity studies of a virus isolated from ticks (Ornithodoros coriaceus) and tick-exposed cattle. Amer. J. Vet. Res. 37:1201-1206.

- Wallis, G.P. and B.R.Miller. 1983. Electrophoretic analysis of the ticks Ornithodoros (Pavlovskella) erraticus and O. (P.) sonrai (Acari: Argasidae). J. Med. Entomol. 20:570-571.
- Walton, G.A. 1953. Ornithodoros moubata in wart-hog and porcupine burrows in Tanganyika Territory. Tran. R. Soc. Trop. Med. Hyg. 47:410-411.
- Walton, G.A. 1957. Observations on biological variation in Ornithodoros moubata Murray (Argasidae) in East Africa. Bull. Ent. Res. 48:669-710.
- Walton, G.A. 1958. Studies on Ornithodoros moubata Murray (Argasidae) in East Africa. Part I. E. Afr. Med. J. 35:57-84.
- Walton, G.A. 1960. The reactions of some variants of Ornithodoros moubata Murray (Argasidae, Ixodoidea) to desiccation. Parasitology 50:81-88.
- Walton, G.A. 1962. The Ornithodoros moubata superspecies problem in relation to human relapsing fever epidemiology. Symposium of the Zoological Society of London. 6:83-156.
- Walton, G.A. 1964. The Ornithodoros "moubata" group of ticks in Africa. Control problems and implications. J. Med. Entomol. 1:53-64.
- Walton, G.A. 1979. A taxonomic review of the Ornithodoros moubata (Murray) 1877 (sensu Walton, 1962) species group in Africa. pages 491-500 in Recent Advances in Acarology. Vol. II. J.G.Rodriguez, (ed.). Academic Press, New York.
- Wardley, R.C., C.de M.Andrade, D.N.Black, F.L.de Castro Portugal, L.Enjuanes, W.R.Hess, C.Mebus, A.Ordas, D.Rutili, J.Sanchez Vizcaino, J.D.Vigario, P.J.Wilkinson, J.F.Moura Nunes and G.Thomson. 1983. African Swine Fever Virus. Arch. Virol.76:73-90.
- Washino, R.K. and C.H.Tempelis. 1983. Mosquito host bloodmeal identification: methodology and data analysis. Ann. Rev. Entomol. 28:179-201.
- Weitz, B. and P.A.Buxton. 1953. The rate of digestion of blood meals of various haematophagus arthropods as determined by the precipitin test. Bull. Entomol. Res. 44:445-450.

Wikel, S.K. 1983. Host immunity to tick bite. pages 249-269 in Vector Research. Vol. 1. K.E.Harris, (ed.). Praeger, New York.

Wilkinson, P.J. 1981. African swine fever. pages 767-786 in Virus Diseases of Food Animals. A world geography of epidemiology and control: disease monographs. Vol. II. E.P.J.Gibbs, (ed). Academic Press, London.

Wilkinson, P.J. and R.C.Wardley. 1982. The epidemiology of African swine fever. pages 2-9 in Proceedings of the 3rd Symposium, Arbovirus research in Australia, Brisbane, February 1982.

Williams, R.E., J.Casals, M.I.Moussa and H.Hoogstraal. 1972. Royal Farm virus: a new tickborne group B agent related to the RSSF complex. Amer. J. Trop. Med. Hyg. 21:582-586.

Woodruff, R.E. 1973. The scarab beetles of Florida (Coleoptera: Scarabaeidae), part I. The Laparostietini (Subfamilies: Scarabaeinae, Aphodiinae, Hybosorinae, Ochodaeinae, Geotrupinae, Acanthocerinae). FL Dept. Agr. & Consumer Serv., Div. Plant Industry. Arthropods of Florida and Neighboring Land Areas. 8:1-220.

Woodruff, R. E. 1982. Arthropods of gopher burrows. pages 24-49 in The Gopher Tortoise and it's Sandhill Habitat. R.Franz and R.J.Bryant, (eds.). 3rd Annual Meeting Gopher Tortoise Council, 30 Oct. 1982. Tall Timbers Research Station, Tallahassee, FL.

Young, F. N. and C. C. Goff 1939. An annotated list of the arthropods found in the burrows of the Florida gopher tortoise, Gopherus polyphemus. (Daudin). Fla. Entomol. 22:53-62.

Yunker, C.E., C.M.Clifford, L.A.Thomas, J.Cory and J.E.George. 1972. Isolation of viruses from swallow ticks, Argas cooleyi in the southwestern United States. Acta Virol. (Prague) 16:415-421.

Yunker, C.E., C.M.Clifford, L.A.Thomas, J.E.Keirans, J.Casals, J.E.George and J.C.Parker. 1977. Sunday Canyon virus, a ungrouped agent from the tick Argas (A.) cooleyi in Texas. Acta Virol. (Prague) 21:36-44.

Yunker, C.E., C.M.Clifford, J.E.Keirans, L.A.Thomas and P.C.A.Rice. 1979. Aransas Bay virus, a new arbovirus of the Upolu serogroup from Ornithodoros capensis (Acari: Argasidae) in coastal Texas. J. Med. Entomol. 16:453-460.

Zaher, M.A., Z.R.Soliman and F.M.Diab. 1977. An experimental study of Borrelia anserina in four species of Argas ticks. 2. Transtadial survival and transovarial transmission. Zeit. Parasitenk. 53:212-223.

Zumpt, F. and D.Organ. 1961. Strains of spirochaetes isolated from Ornithodoros zumpti Heisch and Guggisberg, and from wild rats in the Cape Province: A preliminary note. So. Afr. J. Lab. Clin. Med. 7:31-34.

BIOGRAPHICAL SKETCH

Eric Gordon Milstrey was born on June 13, 1957, in Schenectady, New York. He graduated from Colonie Central High School, Colonie, New York, in June, 1975. In September, 1975, he entered the SUNY College of Environmental Sciences and Forestry. He graduated in June, 1979, receiving a Bachelor of Science degree in wildlife biology.

Through college he worked for several commercial pest control companies in New York and after graduation became the manager of a pest control company in Tampa, Florida.

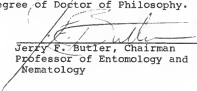
In September, 1981, he began his graduate training at the University of Florida in the Department of Entomology and Nematology. In August, 1983, he received a Master of Science degree for his research on the hydrocarbon pheromones of the horn fly, Haematobia irritans.

He continued his graduate training at the University of Florida working toward a Doctor of Philosophy degree researching the soft tick, Ornithodoros turicata americanus.

He was married in May of 1983 to Susan Alexandra King and their son, Tristan Emory, was born on July 11, 1985.

His entomological training and experience will be utilized after graduation by the US Army Medical Service Corps at Fort Mead, Maryland.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

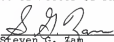


Jerry F. Butler, Chairman
Professor of Entomology and
Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

E. Paul Gibbs
Professor of Immunology and
Medical Microbiology and
Veterinary Medicine

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Steven G. Zam
Professor of Microbiology and
Cell Science

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Jon Allen
Associate Professor of
Entomology and Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

L. Richard Franz
Associate in Natural Sciences

This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

May 1987



Dean, College of Agriculture

Dean, Graduate School

